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The American Midland Naturalist

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The Comparative Internal Morphology of Seeds[1]

A. C. Martin

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Introduction

PERSPECTIVE

Modern botanical science has made tremendous progress in the past 150 years but during this period some phases of botany have remained quiescent. Prominent among the dormant phases is the important field of comparative morphology of seeds. Not since the time of Gaertner, a century and a half ago, has there been any extensive study in the internal organization of seeds. This neglect has served as a handicap not only in identification of seeds and their storage and germination but also in formulation of correct concepts of plant phylogeny and classification since in plants, as in animals, embryos are of fundamental value in denoting relationships. Seeds, like most reproductive structures, are relatively stable; their basic internal organization varies only slightly among related species and genera and the differences that do exist may properly be regarded as significant phylogenetically.

An indication of the state of knowledge in this field is available in current floras. Three principal floras were checked with evidence obtained directly from seeds with the following results: Flora A with internal seed descriptions for

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1 Most of the basic material for this report was part of a doctorate thesis submitted to the George Washington University in December, 1943.

It is a pleasure to acknowledge the material and moral help given by Dr. Robert F. Griggs of George Washington University and the National Research Council and by Mr. Arnold L. Nelson, Director of the Patuxent Research Refuge of the Fish and Wildlife Service, as well as by others of the latter organization.

It should also be acknowledged that the Fish and Wildlife Service was partner in the undertaking to the extent that it made possible the use of essential equipment, including the seed collection, and also furnished the skilled services of Mrs. Katheryne C. Tabb for the inking-in of drawings and Mr. Henry B. Meyers for the lettering of legends.

only two families, both of which were wrong, scored zero; B gave seed descriptions for 141 families and scored 37%, while C committed itself on 112 families and had 46% of them right. The tendency among recent floras to omit statements about seed internals doubtless has been influenced by the inaccuracy of information on the subject.

Joseph Gaertner's classical study, "De Fructibus et Seminibus Plantarum," was issued in two large volumes in 1788 and 1791 and was followed by a relatively small supplement by the son, Carol Gaertner, in 1805. This monumental work is primarily on fruits but its excellent presentation of seed morphology appears to have served as the principal source of information on the subject for subsequent botanical publications. A partial indication of the extent of such use is given in the fact that some of its relatively few errors on seed structure have been transmitted intact to the modern generation of botanical books. Many additional mistakes on seed morphology, some of them apparently occasioned by misinterpretation of Gaertner's original Latin, have also accumulated in present-day literature.

Gaertner's historic contribution to comparative seed morphology differs from the present study in several significant respects. Since his main subject is "carpology," the principal criteria for keys, classification and order of presentation are fruit characters; seeds are secondary. Furthermore Gaertner's classifications are not intended to represent phylogenetic relationships in any degree; they originated nearly seventy years before Darwin expressed his views on evolution and are, therefore, of a comparatively static type. Finally, many of the seed drawings are minute and are too small to permit clear distinction between embryo and endosperm or to show relationship between parts.

There is no other single reference comparable to Gaertner but there is a multitude of other publications from which can be gleaned varying amounts of information on the gross internal characteristics of seeds. Some of these writings are restricted to a single genus or species and some relate to a large share of the plant kingdom. Most, however, of these miscellaneous sources, whether original or not, usually provide fragmentary and unsatisfactory knowledge on seed internals. Many hundreds of reports deal with the embryology of ovules, with the histology of the testa and with the external morphology of economic seeds but these have almost no direct relation to the present study; the myriad of embryological researches are concerned primarily with early stages of ovules rather than with seeds whereas the other two fields deal with neither embryo nor endosperm.

THE PRESENT STUDY

In 1938 a beginning was made on a systematic analysis of the gross internal features of seeds, particularly on the embryo and endosperm and their relative size, shape and position. The work was done largely in evenings and holidays and was completed in 1943. One thousand two hundred and eighty-seven genera of plants were covered, largely from the United States but with considerable representation of specimens from all parts of the world. Results of

the investigation include a system of seed classification, an outline of seed phylogeny and an illustrated, classified, and annotated roster of the genera analyzed.

Since the study has been based on a majority of the recognized plant families of the world it is assumed that the classification plan may be adaptable, in a limited degree, to the flora of the world. Specific application of the classification system to some families in this study is, however, to be regarded as tentative since family position within seed type categories has been assigned on the basis of genera present in the Fish and Wildlife Service seed collection which, in some instances, is a very incomplete world-representation for the family concerned.

With regard to prospective usefulness of this manual to seed identifiers it is freely acknowledged that external features of seeds are, and will continue to be, the principal means of seed identification. Resort to internal characters is advocated not as an independent and adequate basis of identification but as a supplement to determination by external means. To the author, knowledge of internal structure serves as an important, almost indispensable means of ascertaining the general part of the plant kingdom in which an unfamiliar seed belongs and also is a valuable adjunct for verification of determinations based on surface characteristics. It is assumed that this manual will enable others to capitalize on the advantages of this procedure.

METHOD AND MATERIALS

The Fish and Wildlife Service seed collection in the Economic Investigations Laboratory, Patuxent Research Refuge, Bowie, Maryland, served as the source of study materials. This collection has been in the process of development for nearly half a century and is probably one of the best in the world. It contains a good representation of the more common and important native and naturalized plants of the United States and aggregates about 12,000 specimens, 6,000 species and 1,400 genera. In choosing individual specimens for study and illustration preference was given to materials recently collected or in good state of preservation and also to those having evidence of authentic identification. Though the majority of specimens in the seed collection possess suitable collection data and though, in many instances, the identification is supported by herbarium mounts from which seeds were removed, there are numerous other specimens for which correctness of identity cannot be vouched. Danger of error from this source has, however, been reduced by caution exercised in selecting specimens for analysis.

The genus was selected as a primary base for study; species have been cited and illustrated only insofar as they served to typify the genus concerned. Normally genera, regardless of their size in number of species, were sufficiently uniform in internal gross anatomy to permit one specific example to serve for the whole group but frequently it was desirable or necessary to use two or more species in order to represent the genus adequately. Usually all species of a genus in the seed collection were studied before the genus representative

was selected and therefore the number of species indicated as available for study in the roster accompanying the diagrams is, with few exceptions, equivalent to the number actually studied. Species totaling upward of fifty in a genus were studied individually but when, in a stable genus like Carex, the number ran higher, the analysis was confined to a sampling of the more conspicuous types.

Freehand sections were made with razor blades or rarely with hacksaws. Sections of small specimens were made under the microscope. Seeds were cut vertically in a plane calculated to display the embryo to best advantage and additional specimens were cut horizontally near the middle. Generally five to ten (often more) vertical halves and an equal number of horizontal halves of a species were cut and mounted in modelling clay for measurement and for microscopic study preparatory to drawing; fewer sections were made in species and genera studied but not illustrated.

It was found advantageous to immerse in water, sections of non-starchy seeds that did not show clear distinction of internal parts. Ordinarily the water was applied by pipette while the seeds were arranged in suitable position for study on the modelling clay. Usually boundaries of internal areas became much more definite within two or three minutes of soaking but frequently it was desirable to wait longer and tease-out the various parts with dissection needles. In the case of starchy seeds, dilute solutions of iodine caused the endosperm to become very distinct from the embryo.

Measurements of most seeds were made with a micrometer adapted to use immediately over the object rather than in the microscope eyepieces; for large seeds a millimeter rule was employed. Dimensions and to some extent outlines in drawings were obtained by measurement and calculation to avoid distortions frequently induced by camera lucida. A binocular dissecting microscope with magnification of 7, 20, and 30 was used except in rare instances wherein a compound microscope was required.

Illustrations were made for only those genera possessing evident endosperm; other genera were studied but were not drawn except for sketches included with original notes. All drawings consist of combinations of vertical and cross section diagrams of seed contents exclusive of seed coverings. The cross section diagrams (representing approximately median cuts) are intended as supplements to the vertical view; they help assure correct impressions of shape and proportions of parts. All diagrams have been made with the same length (3 cm., in the original) in the long axis of the vertical section in order to facilitate comparison of proportions (embryo and endosperm) on a common denominator of size. Also all seeds, regardless of their natural position in the fruit or on the plant were oriented with the embryo in an erect position or with the radicular end of the stalk pointed downward. In order to make particularly clear the relationship of embryo and endosperm, black and white contrast was used. White was reserved for depiction of endosperm in order to avoid uncertainty in those numerous instances wherein it constitutes a tapering or narrow marginal strip which if indicated in black could not be distinguished readily from the black line outlining the seed.

The drawings are presented in family groups but the arrangement of the families in relation to each other as well as the order of genera within fami-

lies is based wholly on considerations of seed structure—not on any recognized system of plant phylogeny. The criteria used as foundations of the arrangement are based primarily on premises of phylogeny and secondarily on convenient artificial (non-phylogenetic) characters. Slight relative differences between certain genera or certain families necessitated somewhat arbitrary decision as to their comparative position. Furthermore the general sequence of progression of genera within a family might, in some instances, be reversed with just about as much logic as supports the existing arrangement since often it is difficult to decide whether a particular trait represents specialization or primitiveness.

Conservatism ("lumping") and its opposite ("splitting") are both represented in policies on nomenclature though the former is believed dominant. Generic names are almost uniformly of the inclusive type (Polygonum, Euphorbia, etc.) but in a few instances groups treated in this study as families (Mimosaceae, Malaceae, etc.) represent tribes or subfamilies of the more conservative botanists. The "splitting" of these groups seemed advantageous for the purposes of seed study. Taxonomic disagreement among floras and related literature combined with the lack of a comprehensive standard name source has made it difficult to assure nomenclatural accuracy in scientific names used.

DEFINITIONS

Current use of the term endosperm is inconsistent and somewhat confusing. College texts and some other botanical sources define endosperm as a tissue arising within the embryo sac consequent to the triple fusion of polar and sperm nuclei. On the other hand floras incline to disregard the distinction between storage tissue originating inside the embryo sac (endosperm in the strict sense) as contrasted with storage tissues formed outside (perisperm). Some authors use the designation endosperm to cover any and all non-embryonic storage tissue within the seed regardless of whether or not it is partly or wholly perisperm. This loose or inclusive use of the word has become so well-established that its correction, even if desirable, would be difficult. The best alternative appears to be clear recognition of the two distinct usages or meanings of endosperm, one strict and the other broad. In this manual the word is used in the broader sense since commonly it is impossible to distinguish perisperm from true endosperm except by embryological or other histological studies. The designation albumen has fallen into disfavor, apparently because of misleading connotations resulting from comparison to albumen of eggs. Storage tissue was weighed as a new and non-committal name for this purpose but was dropped in favor of endosperm in its inclusive sense.

The simple name *stalk* has been chosen for the stem-like portion of the embryo in preference to the numerous other designations such as hypocotyl, radicle, hypocotyl and radicle, embryonic axis, radicular axis and hypocotyledonary axis that have been used to describe part or all of this structure.

Expressions of size of either embryo or of endosperm generally make definite implications of relative proportions of the other; for example, small embryo implies copious endosperm and copious endosperm implies small embryo. It is

customary to describe embryos as "minute," "small" or "large" and endosperm as "scant" or "copious" but these terms, unfortunately, are ambiguous enough to produce widely divergent interpretations in different minds. To reduce this defect a quantitative classification of embryo size has been devised and used in this study. It consists of five size-designations representing approximately, quarter-unit volumetric proportions of embryo to endosperm and though the method is not precise it is much less indefinite than prevailing terminology and is preferable for classification purposes. (See Fig. 1.) If relative embryo size is expressed on this quarter-unit basis the proportion of endosperm is defined at the same time. Efficient use of the plan requires careful appraisal of embryo-endosperm proportions as revealed in sectioned seeds.

Fig. 1.—Size-designations for embryos.

The designations "endosperm none," "without endosperm" or "exalbuminous" should not be accepted too literally. Many or possibly a majority of the seeds usually classed thus, both in this study and in numerous botanical books, actually have a thin persistent lining of endosperm often consisting in part of perisperm and frequently serving as a semipermeable membrane. Very commonly the layer is one to four cells in thickness and being obscure or indiscernible under low magnification it appears practical to continue the prevailing practice of ignoring the presence of this negligible endosperm in so far as seed identification and classification are concerned.

Classification Plan*

Whereas superficial characteristics of seeds such as of shape, size, color and surface are myriad and often vary markedly among species or genera in the same family, the significant types of internal arrangement incline to be relatively few and comparatively stable. A system of classification based on external characters would necessarily be complex and chaotic in its groupings of unrelated species, genera and families. Though the use of internal characters does not provide immunity from these defects it does assure comparative simplicity and a considerable degree of coherence of related groups.

Categories of classification chosen were purposely limited to a few seemingly basic units that might indicate natural relationships and help to reconstruct the course of seed phylogeny. The embryo was selected as the principal criterion and differences in its shape, size or position have served as the chief foundation for classification. All principal kinds of seeds have been grouped

*See Note on page 529.

under two main categories of classification: *types* and *divisions*. Twelve seed types have been recognized as including all of the basic forms of seeds studied and these twelve units are embraced within three major groupings termed divisions. Some of the classification designations are old names used in a new sense; all three divisional names, Basal, Peripheral and Axile have been employed previously but not as applied to the specific groupings in this study. In the case of the twelve seed types the names are either new—or new as applied to the groups concerned. With two exceptions the seed types appellations are corollary in the sense that they are descriptive of the embryo; in two types, Dwarf and Micro, the names are intended to relate more to the seed as a whole than to the embryo.

The classification categories are outlined with diagrams in Fig. 2 and are defined below in summarized characterizations. Also a key to the types is provided.

CLASSIFICATION UNITS

BASAL DIVISION—Embryos usually relatively small, and restricted to the lower half of the seed—except in some of the Lateral type; seeds usually medium to large; endosperm abundant and generally starchy except in the Rudimentary type. The Capitate and Lateral types include only Monocots but the Rudimentary and Broad types contain both Monocots and Dicots.

Rudimentary—Embryo small, globular to oval-oblong; seeds generally of medium size or larger; cotyledons are usually rudimentary and obscure but sometimes they are evident, making the embryos appear like miniatures of the Linear or Spatulate types. The group is not entirely clear-cut since most of the families concerned have some genera that merge into the Linear type and a few incline toward the Broad.

Broad—Embryo as wide as or wider than high, peripheral or nearly so.

Capitate—Embryo expanded above into head-like form; Monocots only.

Lateral—Embryo basal-lateral or lateral, inclined to expand in the plane of the periphery; small to half or rarely larger. This type includes only the Gramineae but it represents much diversity in embryo size. The name Basal applies well to a majority of the grass genera though Peripheral might seem more suitable for those with expanded embryos.

PERIPHERAL DIVISION—Embryo ordinarily elongate and large, quarter to dominant, contiguous in part at least to the testa and often curved; endosperm (actually perisperm) conspicuously starchy; central or in a few instances lateral. Cotyledons narrow or expanded. Dicots—but in several cases one of the cotyledons is abortive.

Peripheral—Characters of the division.

AXILE DIVISION—Embryo small to total, central (axile) straight, curved, coiled, bent or folded; endosperm not starchy except in five Monocot families of the Linear type. Well-represented in Gymnosperms, Monocots and Dicots; the division includes the Linear, Miniature and Foliate subdivisions.

(LINEAR SUBDIVISION)

Characteristics of the subdivision are those of its only type; well-represented in Gymnosperms, Monocots and Dicots.

Linear—Embryo generally several times longer than broad, straight, curved or coiled; cotyledons not expanded; seed normally not minute.

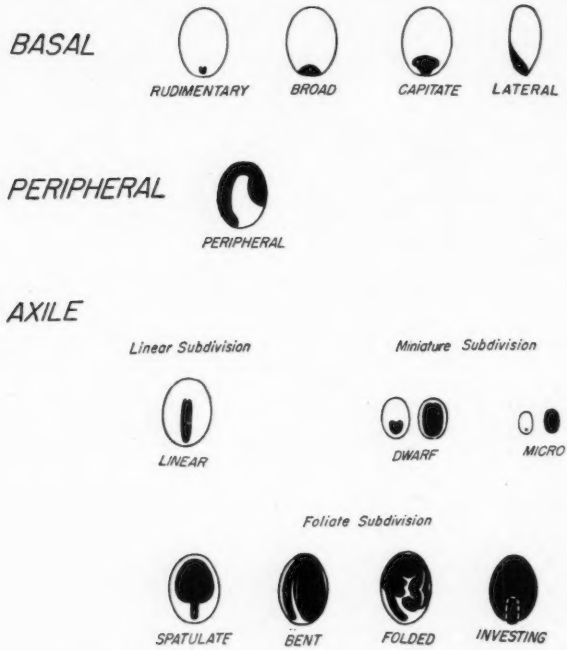


Fig. 2.—The twelve seed types exemplified in diagrams.

(MINIATURE SUBDIVISION)

Seeds small to minute with embryos that are stocky or minute; seed coverings generally delicate and often cellular-reticulate; endosperm not starchy.

Dwarf—Embryo variable in relative size, small to total, generally stocky, usually oval to elliptic or oblong, cotyledons inclined to be poorly developed; seeds small, generally 0.3 mm. to 2 mm. long exclusive of testa, often nearly as broad as long.

Micro—Seeds minute, usually less than 0.2 mm. long exclusive of testa, generally globular and consisting of relatively few cells, approximately 50 to 150 within the testa; embryo minute to total.

(FOLIATE SUBDIVISION)

Embryo large, generally quarter to total, central rather than peripheral; cotyledons expanded; seeds generally medium to large; endosperm not starchy.

Spatulate—Embryo erect; cotyledons variable, thin to thick and slightly expanded to broad.

Bent—Embryo spatulate but bent in jackknife form; cotyledons generally thick.

Folded—Embryo with cotyledons usually thin, extensively expanded and folded in various ways.

Investing—Embryo erect and with thick cotyledons overlapping and encasing the somewhat dwarfed stalk for at least half its length; endosperm wanting or limited.

KEY TO THE TYPES

Endosperm generally present and definitely starchy (endosperm lacking in certain Cactaceae and in Salicornia, Sarcobatus and Salsola which have spirally coiled embryos); embryo peripheral or partly so in relation to endosperm:

- Embryo globular, broader than high, seed globular ..... *Broad*
- Embryo capitate or turbinate ..... *Capitate*
- Embryo basal-lateral or lateral, evident from the exterior ..... *Lateral*
- Embryo evidently dicot (except in Claytonia and Abronia), elongate or large ..... *Peripheral*

Endosperm, if present, not definitely starchy except among a few linear-embryoed forms; embryo not peripheral:

- Embryo minute in medium to large seeds ..... *Rudimentary*
- Embryo of variable relative size in minute seeds having thin reticulated testa:
  - Seed interiors 0.3 to 2 mm. long ..... *Dwarf*
  - Seed interiors less than 0.2 mm. long ..... *Micro*
- Neither embryo nor seed minute:
  - Cotyledon(s) not expanded, embryo linear ..... *Linear*
  - Cotyledons (2) expanded and wider than the stalk:
    - Embryo erect:
      - Stalk not invested by cotyledons or only slightly so ..... *Spatulate*
      - Stalk invested half of length or more ..... *Investing*
    - Embryo jackknife-bent ..... *Bent*
    - Embryo with folded cotyledons ..... *Folded*

Seed Phylogeny

EVOLUTIONARY TRENDS IN SEEDS

Embryo development.—It is widely though not unreservedly assumed that smallness in embryos, as compared to size of endosperm, is representative of a primitive state in seeds and, conversely, that embryos which become well-developed before dormancy reflect a higher evolutionary rank. Fossil seeds (megasporangia) from the Paleozoic era reveal no embryos whatever[1] and there is considerable other evidence from both phylogeny and ontogeny tending to support the concept of relative antiquity of rudimentary embryos. Conspicuous exceptions occur but in general there appears to be considerable conformity. The principle, however, is dangerously incomplete in the absence of an important reservation regarding seed size since a relatively small embryo (in proportion to endosperm) in a small or minute seed may denote just the reverse, a specialized and advanced state, as exemplified by many genera of

[1] Coulter, Barnes & Cowles, A Textbook of Botany, Vol. I, part I, p. 206.

the Miniature subdivision. In general then it may be more correct to assume that medium-sized or large seeds having relatively small embryos are likely to be representative of the primitive type though it should not be implied unequivocally that all seeds of this description are necessarily primitive.

The time of inception of dormancy seems to be the crucial phylogenetic trait related to primitiveness of seeds. Among the ancient groups of plants it would appear that dormancy set in early or at least before development became extensive whereas the more specialized, relatively recent forms (exclusive of the Miniature subdivision) tend to postpone dormancy until the embryo occupies most or all of the seed interior.

Seed size.—From the ancient starting point of primitive seeds to the modern state of flowering plants there appear to be two distinct and strongly divergent lines of progression as regards seed size. The two trends, embracing much of the plant kingdom, represent contrasting principles in the economics of seed production, one stressing quantity and the other quality. Whereas some plants bear myriads of minute more or less delicate seeds, others incline toward the opposite policy of investing their food reserves in relatively few, large, well-developed seeds having advanced types of embryos. Divergent orthogenesis in these opposite directions has produced distinct forms of seeds that are particularly conspicuous in the two Axile subdivisions, the Miniature, representing quantity production and the Foliate, quality. Embryos in Miniature seeds are not only compressed in size and shape but repressed in development whereas the typical "quality" type of seed has a large embryo with well-developed cotyledons. These trends are evident, to some degree, in other groups besides the Miniature and Foliate and their prevalence in various parts of the plant kingdom attests to success through both of the contrasting principles. Both tendencies may manifest themselves in genera of the same family as in the Rubiaceae (Plate 44), Ericaceae (Plate 38), Saxifragaceae (Plate 37) and Hydrophyllaceae (Plate 43). The Miniature form of seeds occurs commonly in capsules on annual plants and the Foliate in achenes and fleshy fruits but conformity in these correlations is only partial.

Endosperm trends.—The Peripheral division together with three types of the Basal division, the Capitate, Lateral and Broad (except for Dioscorea) are unique in that ordinarily they do not occur apart from conspicuously starchy endosperm. Frequently the endosperm is whitish but whether white or glassy it gives the usual starch reaction with iodine. Conversely, conspicuously starchy endosperm is not evident in any seed types besides those mentioned, except for a few Monocots in the Linear type. Thus it appears that two major phylogenetic lines are associated with differences in endosperm; the Peripheral division, together with part of the Basal, is identified with conspicuously starchy endosperm combined with parietal embryo and, in contrast, the Axile division is essentially central-embryoed and its endosperm, when present, is not conspicuously starchy.

Except in the Miniature subdivision, the presence and amount of endosperm is generally not without significance as an indication of stage of advancement in seeds though this criterion seems of secondary consequence as com

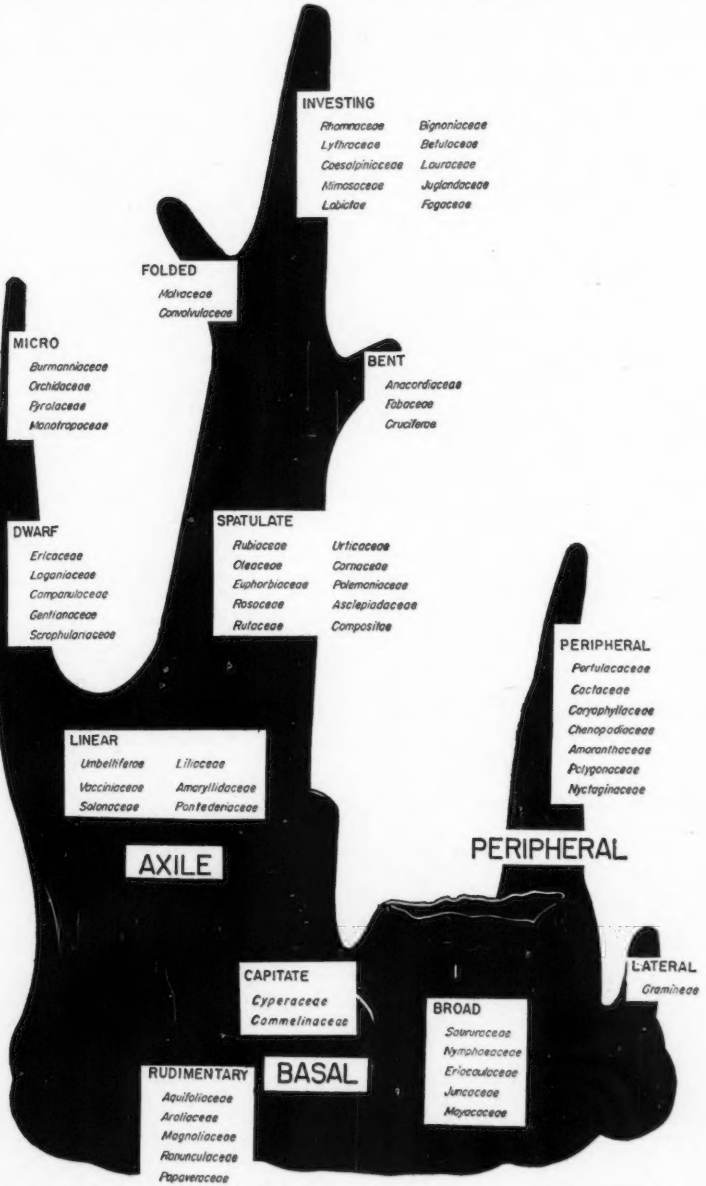


Fig. 3.—Family tree for seed phylogeny, showing some representative families of each type.

pared to embryo characteristics. In fig. 4 it may be noted that there is considerable correlation between reduction in endosperm and progression in the classification system, from Rudimentary to Investing.

Cotyledon development.—In seeds of the Basal division and Miniature subdivision and in some genera of other divisions the cotyledons are inconspicuous and only poorly developed. In the Foliate subdivision (Spatulate, Bent, Folded and Investing types), however, cotyledons show at least the three following developmental trends:

1. Narrow cotyledons expand (Spatulate);

2. Thin cotyledons become folded (Folded type);

3. Thin or medium cotyledons become thick, often absorbing all storage tissue (Bent and Investing types) and frequently growing over and encasing the stalk (Investing type). With progressive growth of the cotyledons the stalk generally becomes proportionately smaller, usually short and broad in vertical forms and slender in bent ones. Extensive development of the cotyledons appears to be at the expense of the stalk as is evident in a comparison of early forms of the Spatulate with the Investing or advanced Bent types.

PHYLOGENY OF SEED TYPES

The family tree for Angiosperm seeds (fig. 3) aims to portray apparent relationships and evolutionary trends in seed types. It is not meant to represent a new family tree for plant classification since a single line of evidence such as the gross internal anatomy of seeds can not be expected to serve adequately as a substitute for correlated phylogenetic information from varied sources. It seems probable that studies in this seemingly neglected field may be instrumental in revising and improving current phylogenetic concepts. For example brief reflection on the distinctive characteristics of seeds of the "Centrospermae" (the Caryophyllales, Polygonales and Chenopodiales) will make one doubt that the conventional classification of these groups as ancestral to other orders is correct.

Gymnosperms were excluded from the diagram for the reason that they are not well adapted to depiction in a family tree for seeds; the group lacks representation in the Basal division and, therefore, would have to be illustrated as a trunk suspended in air or at least separated from its theoretical original base.

The three divisions, Basal, Peripheral and Axile, represent what appear to be the major lines of development in seed phylogeny. In the main these three groups are quite distinct and probably they deserve to wield considerable influence in plant classifications. Comments on them are included in the following discussions on their respective seed types.

The Rudimentary type in its most elementary form probably qualifies better than any other for recognition as progenitor of all other types. Intermediates between it and the Broad type are apparent and there is also clear evidence of ancestral relation of the Rudimentary type to many of the Linear seeds. In fact the combination of Rudimentary, Linear and intermediate forms

in the Ranunculaceae and Umbelliferae has been a complicating factor in the classification of seeds of these families. Also in some instances there is indication of rather direct, short-cut relation between the Rudimentary type and the Foliate sub-group, omitting the usual Linear intermediary. This tendency toward conspicuous and somewhat divergent cotyledons in some of the Rudimentary seeds (Papaveraceae and Ranunculaceae) breaks the homogeneity of their unit to some degree but not sufficiently to seem to warrant its subdivision.

The Broad type is a restricted, rather distinct seed group containing four Monocot and two Dicot families. In it, as in some families of the Capitate and Rudimentary types, the outline of the embryo sac is frequently discernible. If it is conceded that the monocotyledonous characteristic may have originated about this point in plant evolution, the Broad type need not be regarded as an extremely unnatural or illogical assemblage as viewed from the standpoint of systematics, even though it combines Monocots and Dicots. Seeds of the two Broad-type Dicot families, Nymphaeaceae and Saururaceae, seem to show affinity to the Rudimentary type and are probably more primitive than their Monocot counterparts; the latter have embryos that are relatively larger and broader. Though it is possible that the Broad type represents the culmination of a line of progression in seed phylogeny and is a stranded lateral development, it appears more probable that it denotes a somewhat intermediate state between the Rudimentary type and the various derived Monocot and Dicot families having conspicuously starchy endosperm.

Though the grass and sedge families are commonly considered to be closely related to each other, their seeds are quite distinct; indeed the Cyperaceae (Capitate) shows in its somewhat axile-inclined embryo more similarity to Linear and Broad Monocots than it does to the Gramineae (Lateral). Lateral type seeds with elongate embryos might, if provided with two cotyledons, show considerable resemblance to the Peripheral division.

Regardless of whether or not the Broad type is recognized as an ancestral stepping stone, there will necessarily remain extensive phylogenetic gaps between the three semiperipheral Basal types (Broad, Capitate and Lateral) and an even greater hiatus between them and the Peripheral division. These gaps may be necessary in any realistic phylogenetic system of seed classification because they seem to represent historical blanks or missing links in the evolutionary record presented by modern plants. The relative isolation of the Peripheral division from other Dicots seems appropriate since, except for the two-cotyledon habit (which is none too regular in the Nyctaginaceae and Claytonia) this group has more in common with Monocot seed characters than with Dicots. Despite their loosely-knit and somewhat heterogeneous constituency the semiperipheral and peripheral forms seem to be closely related through two important and largely unique traits: peripheral (or nearly peripheral) embryo combined with conspicuously starchy endosperm. The seed phylogeny of Dicots and Monocots having starchy endosperm may be partially explained by the following hypotheses: (1) that the ancestral line which produced the Monocots included intermediate phases having two cotyledons combined with Monocot characters in starchy endosperm and embryo position and

from this source arose the Peripheral group; and (2) much of the ancient parental series disappeared leaving the present phylogenetic orphans: the Peripheral, Broad, Capitate and Lateral types and the few starchy-endospermed Linear Monocots.

The Peripheral division as depicted on the family tree is intentionally arranged to show a large blasted base representing extinct seed types—missing links. The group has been recognized by botanists as a natural coherent unit but to this historic assemblage have been added two families, the Cactaceae and Frankeniaceae. The latter are usually rated much higher in plant classifications but insofar as seeds are concerned, they seem to belong here. The Peripheral division seems to resemble a blind alley leading nowhere beyond itself; though expanded cotyledons in some Peripheral families show at least superficial resemblance to the Foliate subdivision it appears to be a case of "parallelism" in fundamentally distinct groups. Even if the distinct kind of endosperm did not present an insuperable barrier it still would seem almost inconceivable that a peripheral embryo, with its characteristic position *surrounding* the endosperm, could ever have given rise to central-embryoed members of the Axile group.

Linear-embryoed seeds constitute a distinct, readily recognized aggregation that is well represented in the major Spermatophyte subdivisions, the Gymnosperms, Monocots and Dicots. Among seeds of modern Gymnosperms this type is the apparent beginning and, except for Ephedra (Spatulate), the end; for Linear Monocots it represents the apex of progression from the Basal division; for Axile Dicots it is an intermediate stage or a way-station between primitive and advanced seed types. The derivation of Linear Dicots from the Rudimentary type seems obvious and the origin of the Foliate and Miniature subdivisions from erect or nearly straight-embryoed Linear Dicots is also evident, so much so that frequently it is difficult to delimit satisfactorily the two subdivisional branches from the parent trunk. On the other hand the curved or coiled Linear forms (Plates 35 and 36) do not give a clear indication of ancestral parentage to other major seed groups.

The Miniature subdivision is a product of the quantity production trend discussed on page 521. Minute seeds occur in other divisions but ordinarily they lack the characteristics of embryo, endosperm and seed coat that distinguish Miniature seeds. The latter are representative of a somewhat specialized state in seed phylogeny and correspondingly the constituency of the division is largely from families in the upper brackets of the plant kingdom.

The Dwarf type, like the Micro, is complicated somewhat by two phases in embryo size, one inclining toward diminution of the embryo in relation to its endosperm concomitant with reduction of the seed as a whole and the other phase tending toward relatively large or total embryos. The former tendency (small embryo) can be seen in the Campanulaceae, Gentianaceae, Droseraceae and Orbanchaceae and the latter (larger embryo) is to be found in the rest of the Dwarf families. The assumed derivation of the Dwarf type is supported by the fact that there is no sharp demarcation between some Linear and Dwarf seeds. As a consequence arbitrary assignment to one group

or the other has had to be made in certain instances. The family Saxifragaceae is very close to the boundary between the two types. Isolated Dwarf genera also occur in several Linear and Foliate families.

The Micro type though existing in only a limited number of genera is a distinct group characterized by seeds that are minute (0.2 mm. long or shorter, exclusive of testa), often appendaged, and a small to total, poorly developed embryo. Among the four families in which it is represented two occur at the apex of the Monocot series and two in the upper bracket of Dicots. It is assumed that the Micro type represents a more advanced state of the compression and suppression evident in the Dwarf type and the relative classification of the two is based on this premise. The assumed relationship of the Micro and Dwarf types is provided some support by the fact that the Monotropaceae and Pyrolaceae (both Micro) are normally classed as closely affiliated to the Ericaceae (Dwarf). Intermediate forms between these two types are not plentiful in the families and genera studied, but Scoparia, Conobea, Lindernia and some other Scrophulariaceae strongly suggest advancement towards the Micro state from the Dwarf.

The Foliate subdivision represents the acme of embryo development in seeds. In some instances the broad cotyledons have distinct midribs and veins and frequently the plumule with normal first leaves is clearly evident in specimens lacking endosperm. Commonly the width of cotyledons is without conformity in corresponding relative width of the true leaves. Within the Foliate subdivision there are three fairly definite lines of cotyledonary progression (see page 524).

Spatulate seeds appear to have originated through two lines, one from the Linear and the other more directly from the Rudimentary type. To some degree at least there appears to be distinction between Spatulate seeds derived from these two sources, those developed from the Linear type often inclining to have thick cotyledons whereas those that appear more closely related to the Rudimentary type usually have thin cotyledons. This difference in thickness of cotyledons, whether or not the intimation of its origin is correct, does appear to be significant in explaining the derivation of the Folded, Bent and Investing types from the Spatulate; the Folded type, no matter in what manner the cotyledons are arranged, probably originates largely from thin-cotyledoned Spatulate (or Bent) seeds whereas typical Bent and Investing seeds seem to be developed from progressively thickened cotyledons.

Diagrams and Classified Lists of Families and Genera Studied

In the following presentation of drawings and text the three major seed plant groups, Gymnosperms, Monocots and Dicots, are treated separately in order to preserve their group identity. Families also are retained intact though their genera, in some instances, may be referable to two or more seed types. In the latter case the name of the proper seed type is given parenthetically in the left hand margin and the exceptional genus is also recorded in the "Supplement" for the type concerned. The drawings and text are arranged in progres-

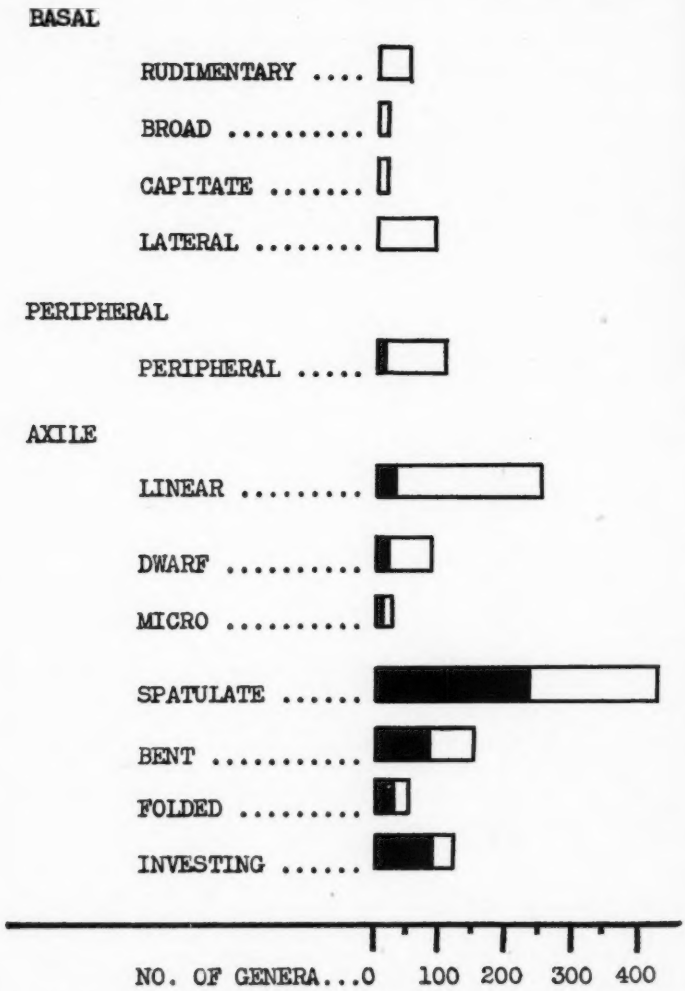


Fig. 4.—Number of genera in all seed types having endosperm (white blocks) and lacking endosperm (black blocks). Definite progression toward non-endospermous condition is evident among genera of the higher seed types.

sive sequence (within each of the three major plant groups) in conformity to the seed classification outlined on page 520.

In the annotated roster, families having endosperm in some or all genera, are, with few exceptions, listed in the same order as their illustrations; families without endosperm (not illustrated) are asterisked and are arranged in alphabetical sequence following the endospermous families of the type concerned. Genera are arranged alphabetically within two categories: those with endosperm and those without endosperm, the lattter being asterisked.

Parenthetical figures following generic names denote the number of species that were available for examination, and, as explained under "Methods" on page 516, this number is usually equivalent to the number of species actually studied in the genus. The absence of parenthetical figures after generic names usually indicates that only one species was studied but in the supplements occurring at the conclusion of most types, there has been no repetition of species enumerations and therefore the absence of figures here has no special significance. Ordinarily, in genera represented by one illustration the genus is fairly uniform in regard to embryo development, unless there is comment to the contrary.

The roster text is arranged to face or accompany closely the plate or plates to which it pertains. Ready reference to the location of individual illustrations on the facing plate is provided after scientific names, the Roman numeral referring to the horizontal row (top to bottom) and the arabic denoting position in the row (left to right).

The three principal parts of the roster are:

Gymnospermae ..... pp. 530-531
Monocotyledones 532-551
Dicotyledones 552-646

NOTE

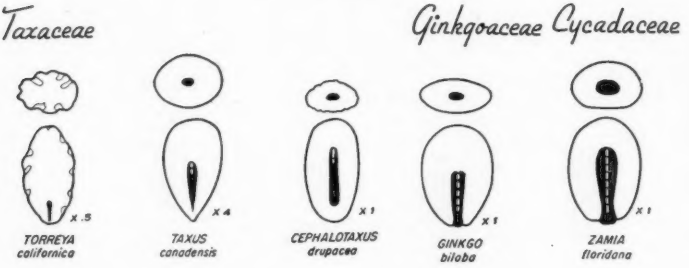
Since the time that this manuscript was submitted, about a year ago, the author has adopted a slightly modified classification. In it the three divisions have been replaced by two by merging the Basal division, except for the Rudimentary type, into an enlarged Peripheral division. The resulting two divisions, Peripheral and Axile, seem to represent well the two main lines of seed evolution.

Gymnospermae

PLATE 1

The Gymnosperms, classed as Linear except for Ephedra, include certain groups that seem to border closely on the Spatulate. However, some of the conifers are less advanced than might be apparent since in a number of cases the somewhat expanded upper part of the embryo consists of several slender cotyledons. The cotyledons of Ginkgo and Zamia are only slightly expanded but it is noteworthy that they are relatively elongate on a short embryo stalk. The endosperm of Gymnsperms is fleshy or oily-fleshy. The absence of Basal forms in present-day Gymnosperms studied precludes an integrated series of progressive stages in evolutionary seed development of the group.

LINEAR



Taxaceae—The seeds of this family are the most primitive type studied among Gymnosperms. Not only are its seeds large with relatively small embryos but in addition the cotyledons are poorly developed as compared to other Gymnosperm families.

Cephalotaxus (2 sp.) *drupacea* Sieb. & Zucc.
Taxus (5 sp.) *canadensis* Marsh.
Torreya (2 sp.) *californica* Torr.
Ginkgoaceae—*Ginkgo biloba* L.
Cycadaceae—*Zamia floridana* DC.

PLATE 2

Pinaceae—Diagrams for genera in this family have been arranged in an approximate progression relating to embryo size, small to dominant. There may be, however, equally good argument for placing at the top those genera such as Thuja, Libocedrus and Chamaecyparis in which the embryo is somewhat spatulate outlined though possessing only two cotyledons.

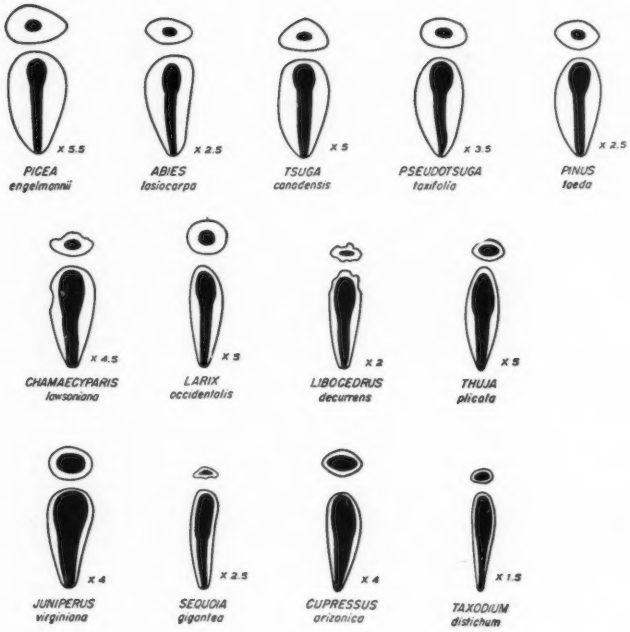
Abies (23 sp.) *lasiocarpa* (Hook.) Nutt.;
Chamaecyparis (5 sp.) *lawsoniana* Parl.
Cupressus (12 sp.) *arizonica* Greene
Juniperus (16 sp.) *virginiana* L.
Larix (6 sp.) *occidentalis* Nutt.
Libocedrus decurrens Torr.
Picea (14 sp.) *engelmannii* (Parry) Engelm.
Pinus (51 sp.) *taeda* L.
Pseudotsuga (2 sp.) *taxifolia* (Lam.) Britton
Sequoia (2 sp.) *gigantea* (Lindl.) Decne.
Taxodium (2 sp.) *distichum* (L.) Rich.
Thuja (3 sp.) *plicata* Donn
Tsuga (6 sp.) *canadensis* (L.) Carr.

SPATULATE

Gnetaceae—*Ephedra* (2 sp.) *viridis* Cov.

PLATE 2

Pinaceae

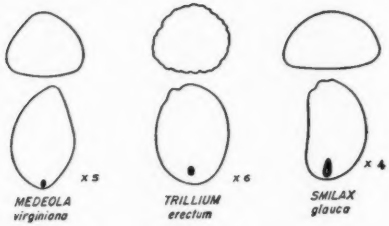


Gnetaceae

Monocotyledones PLATE 3

RUDIMENTARY

Smilacaceae



Smilacaceae—The embryos of Medeola and Trillium belong clearly to the Rudimentary type but Smilax shows inclination toward the Linear type of embryo characteristic of the Liliaceae and in which the Smilacaceae is frequently included. The endosperm is hard and semitransparent.

Medeola virginiana L.
Trillium (sp.) *erectum* L.

Smilax (14 sp.) *glauca* Walt. (LINEAR).

Haemodoraceae

Haemodoraceae—*Lachanthes tinctoria* (Walt.) Ell. Except for difference in size of embryo the internal appearance of this genus resembles Scleria. The endosperm is hard and semitransparent.

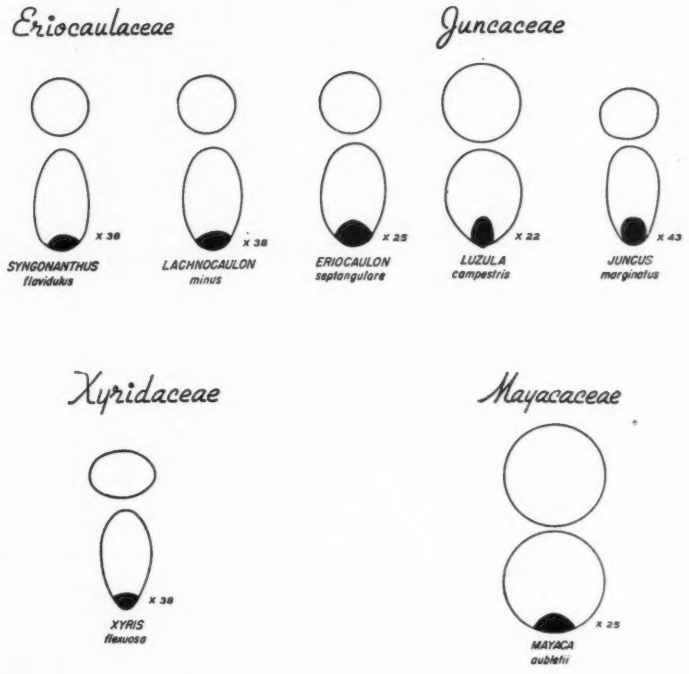
SUPPLEMENT; RUDIMENTARY GENERA (MONOCOTYLEDONES) IN NON-RUDIMENTARY FAMILIES

Liliaceae (Linear)—*Erythronium.*

Palmae (Linear)—*Ptychosperma.*

PLATE 4

BROAD



Monocotyledones of the Broad type show resemblance to the Cyperaceae (Capitate type) and in this connection the Juncaceae seem to serve as an intermediate link. Endosperm in all is starchy.

Eriocaulaceae — *Eriocaulon* (2 sp.) *septangulare* With.
Lachnocaulon minus (Chapm.) Small
Syngonanthus flavidus (Michx.) Ruhl.

Juncaceae—*Juncus* (32 sp.) *marginatus* Rostk.
Luzula (4 sp.) *campestris* (L.) DC.

Xyridaceae—*Xyris* (6 sp.) *flexuosa* Muhl.

Mayacaceae—*Mayaca aubletti* Michx.

SUPPLEMENT; BROAD GENERA (MONOCOTYLEDONES) IN NON-BROAD FAMILIES

Cyperaceae (Capitate)—*Eriophorum, Hemicarpha, Lipocarpha, Mariscus.*
Commelinaceae (Capitate)—*Aneilema.*

PLATE 5

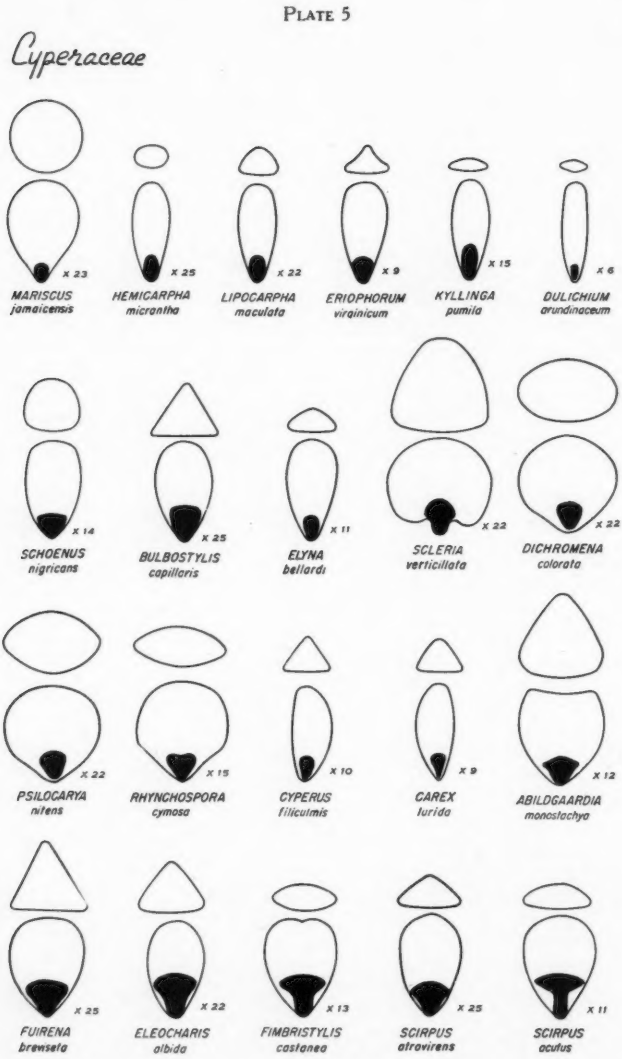

Cyperaceae
x 23
MARISCUS
jamaicensis
x 25
HEMICARPHA
micrantha
x 22
LIPOCARPHA
maculata
x 9
ERIOPHORUM
virginicum
x 15
KYLLINGA
pumila
x 6
DULICHIUM
arundinaceum
x 14
SCHOENUS
nigricans
x 25
BULBOSTYLIS
capillaris
x 11
ELYNA
bellardi
x 22
SCLERIA
verticillata
x 22
DICHROMENA
colorata
x 22
PSILOCARYA
nitens
x 15
RHYNCHOSPORA
cymosa
x 10
CYPERUS
filiculmis
x 9
CAREX
lurida
x 12
ABILDGAARDIA
monostachya
x 25
FUIRENA
breweri
x 22
ELEOCHARIS
albida
x 13
FIMBRISTYLIS
castanea
x 25
SCIRPUS
atrovirens
x 11
SCIRPUS
acutus

PLATE 5

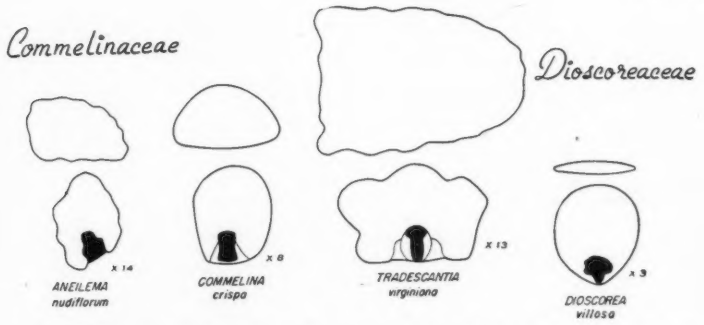
CAPITATE

Except for the Dioscoreaceae the families in this type have starchy endosperm.

Cyperaceae—Though the family is classed as Capitate, two other types are also present: a number of genera (Mariscus, Hemicarpha, Lipocarphya and Eriophorum) have embryos that show relationship to the Broad or Rudimentary types while Dulichium and Kyllinga tend toward the Linear type. The outline of the embryo sac is frequently evident a short distance beyond the embryo. The endosperm is either granular or firm and semitransparent.

Abildgaardia monostachya (L.) Vahl; row III, 5.
Bulbostylis (5 sp.) *capillaris* (L.) C. B. Clarke;
Carex (139 sp.) *lurida* Wahl.; row III, 4.
Cyperus (45 sp.) *fuliculmis* Vahl; row III, 3.—Genus not wholly uniform; embryo varies some in size; inclines to be relatively large in small lenticular species and also in *C. esculentus.*
Dichromena (2 sp.) *colorata* (L.) Hitch.; row II, 5.
Dulichium arundinaceum (L.) Britton; row I, 6. (LINEAR).
Eleocharis (26 sp.) *albida* Torr.; row IV, 2.
Elyna bellardi (All.) C. Koch; row II, 3.
Eriophorum (3 sp.) *virginicum* L.; row I, 4.
Fimbristylis (8 sp.) *castanea* (Michx.) Vahl; row IV, 3.
Fuirena (4 sp.) *breviseta* Cov.; row IV, 1.
Hemicarpha (2 sp.) *micrantha* (Vahl) Wood; row I, 2. (BROAD).
Kyllinga (2 sp.) *pumila* Michx.; row I, 5. (LINEAR).
Lipocarpha maculata (Michx.) Torr.; row I, 3. (BROAD).
Mariscus (3 sp.) *jamaicensis* (Crantz) Britton; row I, 1. (BROAD).
Psilocarya (2 sp.) *nitens* (Vahl) Wood; row III, 1.
Rhynchospora (36 sp.) *cymosa* Ell.; row III, 2.
Schoenus nigricans L.; row II, 1.
Scirpus (33 sp.) row IV, 4, 5; *acutus* Muhl., *atrovirens* Muhl. Small-achened species incline to resemble *S. atrovirens*; larger ones, *S. acutus.*
Scleria (12 sp.) *verticillata* Muhl.; row II, 4.

PLATE 6



Commelinaceae—Tradescantia is the only genus in the family having a distinctly capitate embryo though Commelina is intermediate; Aneilema is somewhat the opposite of capitate in its embryo and resembles the Broad type.

Aneilema nudiflorum (L.) Kunth (BROAD)
Commelina (8 sp.) *crispa* Wooton
Tradescantia (3 sp.) *virginiana* L.

Dioscoreaceae—*Dioscorea* (3 sp.) *villosa* L.

PLATE 6 (Continued)

CAPITATE

Musaceae — *Ravenala madagascariensis* Gmel.

PLATE 7

LATERAL

Gramineae—Standard descriptions of the grass family refer to the embryo as small and basal which as plates 10 and 11 indicate is not correct. The endosperm though normally giving a positive starch reaction varies from fleshy to flinty hardness: in most of the genera it is firm to hard and somewhat translucent. In six genera having very small embryos, Limnodea, Koeleria, Holcus, Sphenopholis, Cinna and Beckmannia and one with embryo slightly larger, Alopecurus, the endosperm is soft-fleshy in consistency. Not infrequently the harder form of endosperm is broken into granular units.

Agropyron (12 sp.) *smithii* Rydb.; row III, 5.
Aira caryophyllea L.; row IV, 4.
Anthoxanthum (3 sp.) *odoratum* L.; row IV, 1.
Arundinaria (2 sp.) *tecta* (Walt.) Muhl.; row I, 5.
Brachyelytrum erectum (Schreb.) Beauv.; row II, 1.
Brachypodium pinnatum (L.) Beauv.; row II, 6.
Bromus (25 sp.) *commutatus* Schrad.; row II, 3.
Cinna (2 sp.) *arundinacea* L.; row IV, 6.
Cynosurus cristatus L.; row IV, 3.
Elymus (15 sp.) *mollis* Trin.; row II, 4.
Festuca (14 sp.) *octoflora* Walt.; row II, 2.
Fluminea festucacea (Willd.) Hitch.; row I, 6.
Gymnopogon ambiguus (Michx.) B.S.P.; row III, 2.
Holcus (2 sp.) *lanatus* L.; row IV, 2.
Hordeum (6 sp.) *jubatum* L.; row III, 1.
Hystrix patula Moench; row II, 5.
Koeleria cristata (L.) Pers.; row I, 3.
Limnodea arkansana (Nutt.) L. H Dewey; row I, 1.
Lolium (4 sp.) *temulentum* L.; row III, 4.
Melica (8 sp.) *californica* Scribn.; row III, 4.
Schizachne purpurascens (Torr.) Swallen; row I, 4.
Sitanion (3 sp.) *jubatum* J. G. Smith: row III, 3.
Sphenopholis (3 sp.) *obtusata* (Michx.) Scribn.; row IV,5.
Trisetum (2 sp.) *spicatum* (L.) Richt.; row I, 2.

PLATE 7

Gramineae

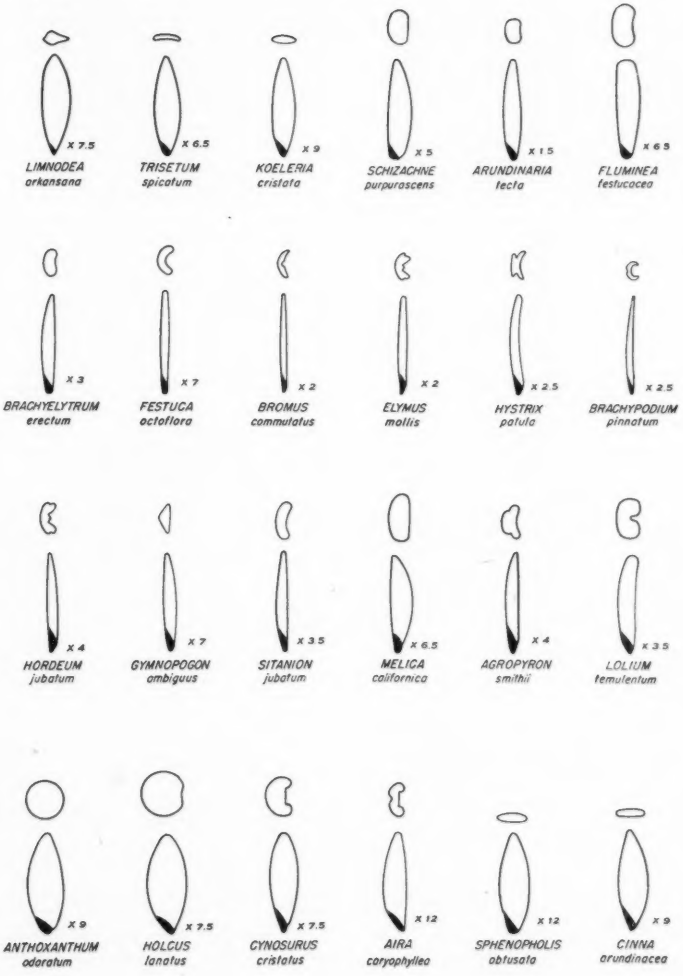
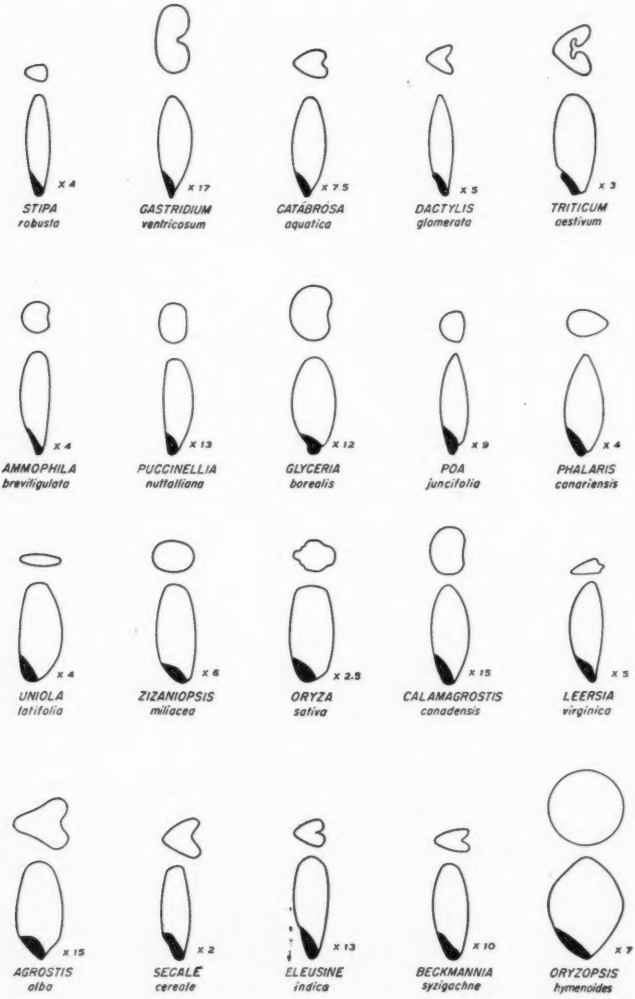


PLATE 8

Gramineae Cont.



GRAMINEAE LATERAL PLATE 8

Agrostis (8 sp.) *alba* L.; row IV, 1.
Ammophila (2 sp.) *breviligulata* Fern.; row II, 1.
Beckmannia syzigachne (Steud.) Fern.; row IV, 4.
Calamagrostris (3 sp.) *canadensis* (Michx.) Beauv.; row III, 4.
Calabrosa aquatica (L.) Beauv.; row I, 3.
Dactylis glomerata L.; row I, 4.
Eleusine (2 sp.) *indica* (L.) Gaertn.; row IV, 3.
Gastridium ventricosum (Gouan) Schinz & Thell.; row I, 2.
Glyceria (9 sp.) *borealis* (Nash) Batchelder; row II, 3.
Leersia (4 sp.) *virginica* Willd.; row III, 5.
Oryza sativa L.; row III, 3.
Oryzopsis (4 sp.) *hymenoides* (Roem. & Schult.) Ricker; row IV, 5.
Phalaris (7 sp.) *canariensis* L.; row II, 5.
Poa (16 sp.) *juncifolia* Scribn.; row II, 4.
Puccinellia nuttalliana (Schult.) Hitch.; row II, 2.
Secale cereale L.; row IV, 2.
Stipa (12 sp.) *robusta* Scribn.; row I, 1.
Triticum (7 sp.) *aestivum* L.; row I, 5.
Uniola (4 sp.) *latifolia* Michx.; row III, 1.
Zizaniopsis miliacea (Michx.) Doell & Aschers.; row III, 2. Though both Zizania and Zizaniopsis have unisexual flowers and are classed as closely related, the seeds of these two genera are very unlike and seem to contradict the assumed affinity.

PLATE 9

Alopecurus (5 sp.) *myosuroides* Huds.; row IV, 5.
Andropogon (11 sp.) *virginicus* L.; row IV, 4.
Arrhenatherum elatius (L.) Mert. & Koch; row I, 2.
Avena (4 sp.) *sativa* L.; row I, 3.
Axonopus (2 sp.) *compressus* (Sw.) Beauv.; row II, 4.
Briza (2 sp.) *minor* L.; row III, 5.
Danthonia (3 sp.) *spicata* (L.) Beauv.; row I, 5.
Deschampsia (5 sp.) *caespitosa* (L.) Beauv.; row II, 3.
Digitaria (6 sp.) *sanguinalis* (L.) Scop.; row III, 2.
Eragrostis (16 sp.) *pectinacea* (Michx.) Nees; row III, 4.
Leptoloma cognatum (Schult.) Chase; row III, 1.
Muhlenbergia (16 sp.) *schreberi* Gmel.; row I, 4.
Paspalum (25 sp.) *floridanum* Michx.; row II, 5.
Phleum pratense L.; row III, 3.
Polypogon (4 sp.) *monspeliensis* (L.) Desf.; row I, 1.
Sacciolepis striata (L.) Nash; row IV, 1.
Trichachne (3 sp.) *insularis* (L.) Nees; row IV, 3.
Trichloris pluriflora Fourn.; row II, 2.
Trichoneura elegans Swallen; row II, 1.
Triplasis purpurea (Walt.) Chapm.; row IV, 2.

PLATE 10

Aristida (10 sp.) *longespica* Poir.; row IV, 4.
Brachiaria (2 sp.) *ciliatissima* (Buckl.) Chase; row IV, 1.
Calamovilfa (2 sp.) *longifolia* (Hook.) Scribn.; row IV, 3.
Chloris (9 sp.) *cucullata* Bisch.; row III, 3.
Cynodon dactylon (L.) Pers. row I, 1.
Dactyloctenium aegyptium (L.) Richt.; row II, 2.
Distichlis (3 sp.) *spicata* (L.) Greene; row II, 1.
Echinochloa (4 sp.) *colonum* L. Link; row III, 5.
Erianthus (4 sp.) *contortus* Ell.; row I, 3.
Eriochloa (5 sp.) *sericea* (Scheele) Munro; row IV, 2.
Leptochloa (6 sp.) *fascicularis* (Lam.) Gray; row III, 2.
Monanthochloe littoralis Engelm.; row I, 5.
Munroa squarrosa (Nutt.) Torr.; row III, 1.
Panicum (64 sp.) *anceps* Michx.; row I, 2.
Sorghum (3 sp.) *halepense* (L.) Pers.; row III, 4.
Sporobolus (11 sp.) row II, 3, 4, 5; *cryptandrus* (Torr.) Gray, *asper* (Michx.) Kunth, *heterolepis* Gray.—*S. cryptandrus* is fairly typical for most of the genus.
Triodia (12 sp.) *flava* (L.) Smyth; row I, 4.
Zizania (2 sp.) *aquatica* L.; row IV, 5.

PLATE 9

Gramineae Cont.

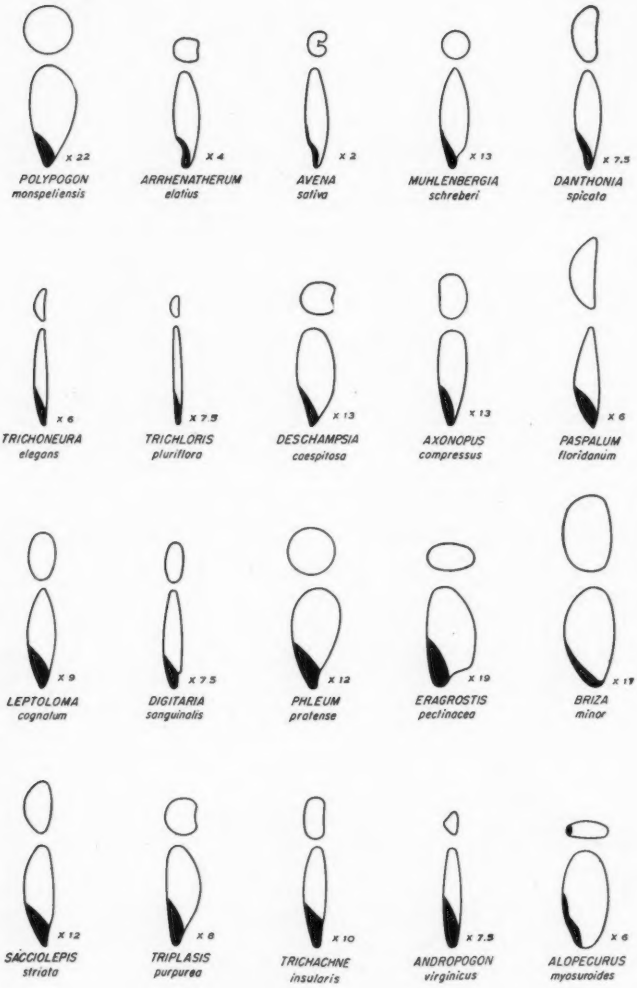
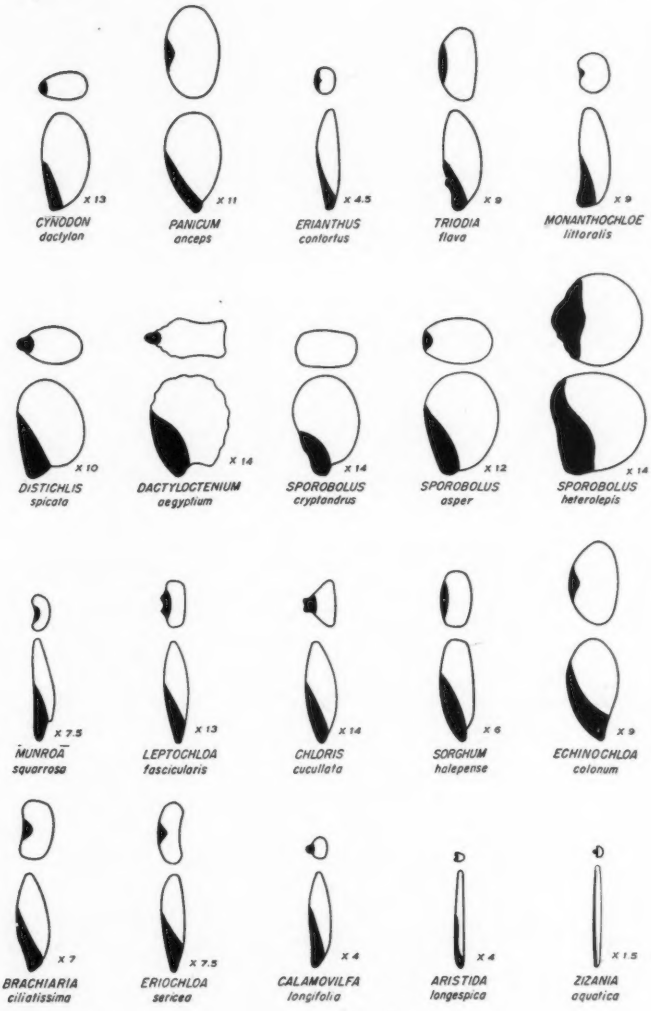


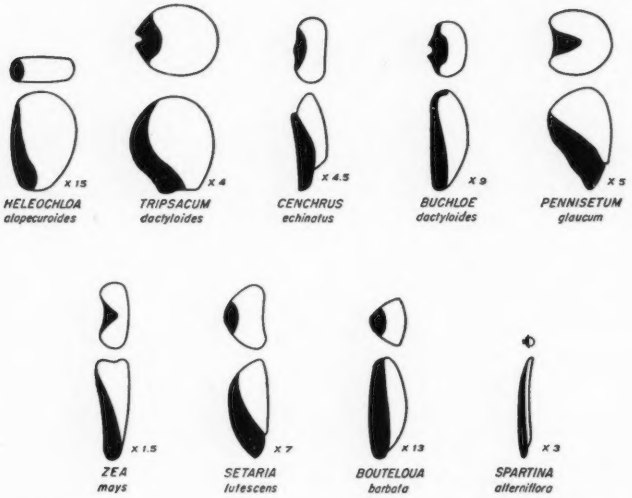
PLATE 10

Gramineae Cont.



LATERAL. PLATE 11

Gramineae Concl.



GRAMINEAE, concl.—

Bouteloua (11 sp.) *barbata* Lag.; row II, 3.

Buchloe dactyloides (Nutt.) Engelm.; row I, 4.

Cenchrus (4 sp.) *echinatus* L.; row I, 3.

Heleochloa alopecuroides (Pill. & Mitterp.) Host; row I, 1.

Pennisetum glaucum (L.) R. Br.; row I, 5.

Setaria (10 sp.) *lutescens* (Weigel) F. T. Hubb.; row II, 2.

Spartina (9 sp.) *alterniflora* Lois.; row II, 4.

Tripsacum dactyloides (L.) L.; row I, 2.

Zea mays L.; row II, 1.

PLATE 12

LINEAR

Palmae—With the exception of Roystonea the embryos of seeds of this family represent a borderline state and are not typically Linear; in fact they show nearly as much resemblance to the Rudimentary and Broad types as to the Linear. The endosperm in all cases is hard and usually semitransparent; it does not give an evident starch reaction.

Archontophoenix alexandrae Wendl. & Drude; row II, 2.

Coccothrinax argentea (Lodd.) Sarg.; row II, 3.

Paurotis wrightii (Griseb.) Britton; row III, 2.

Phoenix (2 sp.) *canariensis* Chaub.; row I, 3.

Ptychosperma elegans Blume; row I, 1.

(RUDIMENTARY).

Roystonea regia O. F. Cook; row IV.

Sabal (2 sp.) *minor* (Jacq.) Pers.; row III, 3.

Serenoa repens (Hart.) Small; row II, 1.

Thrinax (2 sp.) *microcarpa* Sarg.; row I, 2.

Washingtonia filifera (Linden) Wendl.; row III, 1.

PLATE 12

Palmae

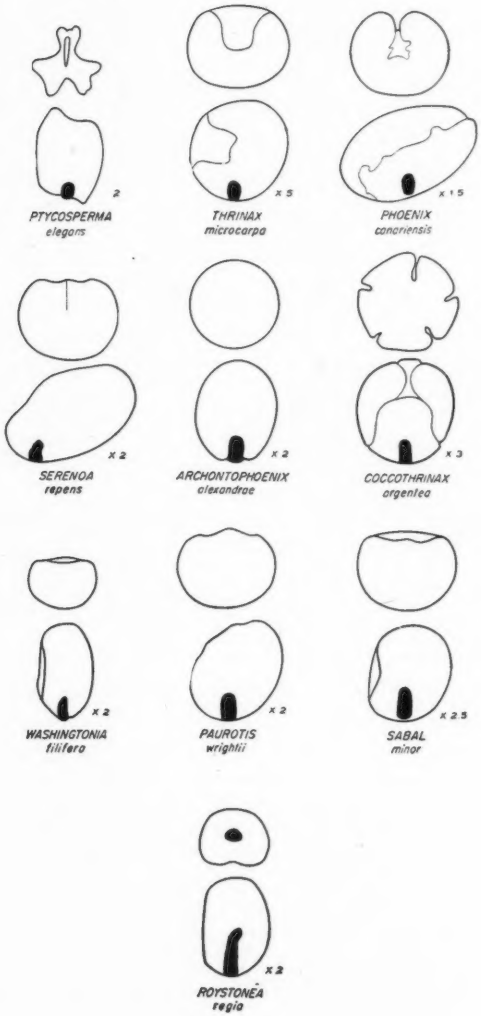


PLATE 13

LINEAR

Convallariaceae—As in the Smilacaceae and Palmae the seeds of this family have hard semitransparent non-starchy endosperm.

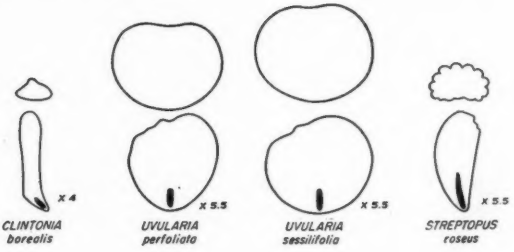
Asparagus (2 sp.) *officinalis* L.; row II, 5.
Clintonia (3 sp.) *borealis* (Ait.) Raf.; row I, 1.
Disporum (2 sp.) *trachycarpum* Wats.; row II, 1.
Maianthemum (2 sp.) *canadense* Desf.; row II, 3.
Polygonatum (2 sp.) *commutatum* (R. & S.) Dietr.; row II, 2.
Smilacina (4 sp.) *stellata* (L.) Desf.; row II, 4. — In *S. racemosa* the embryo is short as compared to *S. stellata, trifolia* and *sessilifolia.*
Streptopus (2 sp.) *roseus* Michx.; row I, 4.
Uvularia (2 sp.) row I, 2, 3; *perfoliata* L., *sessilifolia* L. — *U. sessilifolia* is frequently classed in a separate genus, Oakesia.

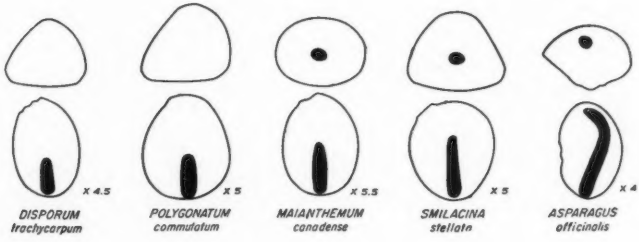
Melanthaceae—The endosperm in this family varies from firm to hard except for Xerophyllum in which it is somewhat fleshy.

Amianthium muscaetoxicum (Walt.) Gray; row III, 1.
Tofieldia (2 sp.) *glutinosa* (Michx.) Pers.; row III, 5.
Veratrum viride Ait.; row III, 3.
Xerophyllum (3 sp.) *douglasii* Wats.; row III, 2.
Zygadenus fremontii Torr.; row III, 4. This species shows a very unusual instability; its embryo varies considerably in size and shape.

PLATE 13

Convallariaceae





Melanthaceae

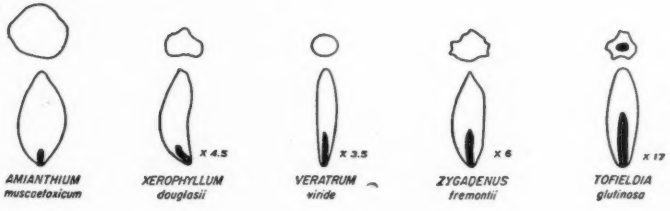


PLATE 14

LINEAR

Liliaceae—In this family Erythronium is the only genus studied that is not definitely Linear in its embryo; it is intermediate between Rudimentary and Linear. Though in numerous genera the embryo extends nearly the length of the seed interior, it still is relatively small and occupies less than a quarter of the seed volume. The endosperm is generally firm to hard and semitransparent and is not starchy.

Allium (8 sp.) *stellatum* Ker; row IV, 3.
Brodiaea (6 sp.) *laxa* (Benth.) Wats.; row II ,2.
Calochortus (7 sp.) *eurycarpus* Wats.; row I, 3.
Camassia scilloides (Raf.) Cory; row III, 4.
Chlorogalum pomeridianum (Ker) Kunth; row IV, 4.
Cordyline australis Hook.; row IV, 5.
Dasylirion (2 sp.) *leiophyllum* Engelm.; row III, 3.
Erythronium (5 sp.) *grandiflorum* Pursh; row I, 1. (RUDIMENTARY).
Leucocrinum montanum Nutt.; row III, 1.
Lilium (9 sp.) *michiganense* Farw.; row II, 1.
Muscari racemosum (L.) Mill.; row III, 2.
Narthecium americanum Ker; row I, 2.
Nolina microcarpa Wats.; row II, 4.
Nothoscordum bivalve (L.) Britton; row I, 4.
Ornithogalum umbellatum L.; row II, 3.
Urginea scilla Steinh.; row IV, 2.
Yucca (10 sp.) *baccata* Torr.; row IV, 1.

PLATE 14

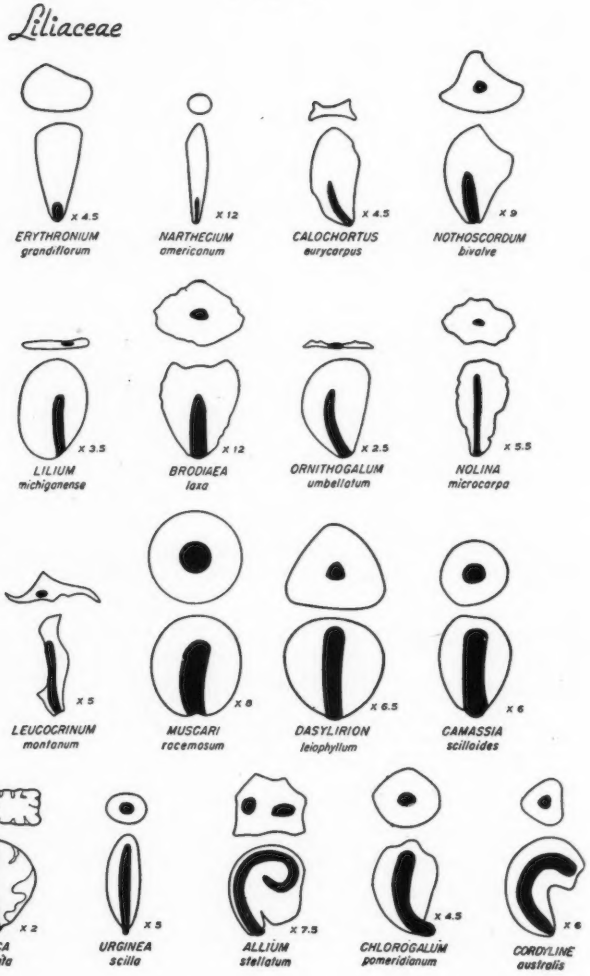

Liliaceae
x 4.5
ERYTHRONIUM grandiflorum
x 12
NARTHECIUM americanum
x 4.5
CALOCHORTUS eurycarpus
x 9
NOTHOSCORDUM bivalve
x 3.5
LILIUM michiganense
x 12
BRODIAEA laxa
x 2.5
ORNITHOGALUM umbellatum
x 5.5
NOLINA microcarpa
x 5
LEUCOCRINUM montanum
x 8
MUSCARI racemosum
x 6.5
DASYLIRION leiophyllum
x 6
CAMASSIA scilloides
x 2
YUCCA baccata
x 5
URGINEA scilla
x 7.5
ALLIUM stellatum
x 4.5
CHLOROGALUM pomeridianum
x 6
CORDYLINE australis

PLATE 15

LINEAR

A distinct subgroup in the Linear type consists of the five families: Cannaceae, Zingiberaceae, Marantaceae, Sparganiaceae and Pontederiaceae (Plates 15 and 16). These are unique, for Linear seeds, in having starchy endosperm and also in having the base of the embryo extend into a depression or cup at one end of the seed—a characteristic noticeable also in the Palmae and Commelinaceae.

Iridaceae—The Iridaceae and Amaryllidaceae resemble closely the Liliaceae in embryo characteristics as well as in nature of endosperm.

Belamcanda chinensis (L.) DC.; row I, 4.
Gladiolus gandavensis Van Houtte; row I, 3.
Iris (10 sp.) *virginica* L.; row I, 5. — There is considerable variation in height and width of embryos in different species; *I. virginica* is nearly average.
Sisyrinchium (5 sp.) *bellum* Wats.; row I, 2.
Tigridia pavonia Ker; row I, 1.

Amaryllidaceae—(See comment under Iridaceae.)

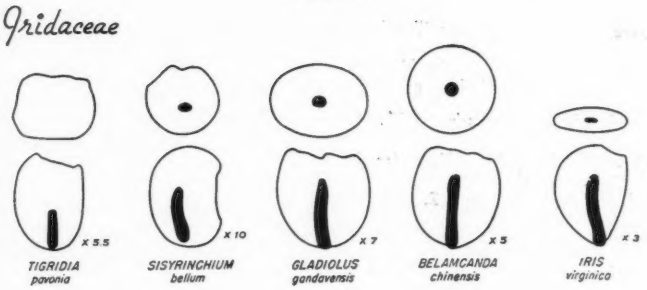
Agave (2 sp.) *virginica* L.; row II, 4.
Amaryllis belladonna L.; row II, 2.
Hypoxis hirsuta (L.) Cov.; row II, 3.
Zephyranthes atamasco (L.) Herbert; row II, 1.

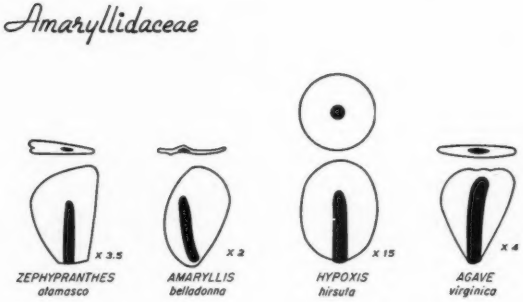
Cannaceae—*Canna flaccida* Salisb.; row III, 1.

Zingiberaceae—*Amomum melegueta* Roscoe; row III, 2.

Marantaceae—*Thalia dealbata* Roscoe; row III, 3.

PLATE 15


Iridaceae
x 5.5
TIGRIDIA
pavonia
x 10
SISYRINCHIUM
bellum
x 7
GLADIOLUS
gandavensis
x 5
BELAMCANDA
chinensis
x 3
IRIS
virginica


Amaryllidaceae
x 3.5
ZEPHYRANTHES
atamasco
x 2
AMARYLLIS
belladonna
x 15
HYPOXIS
hirsuta
x 4
AGAVE
virginica

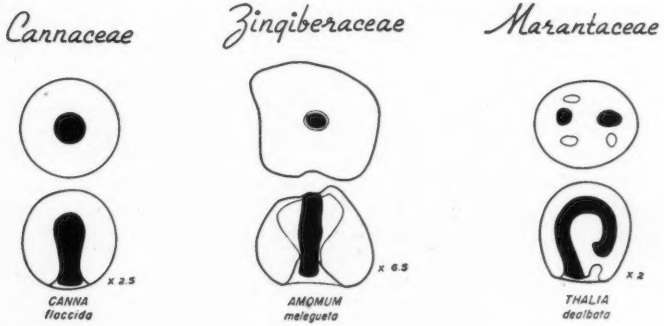

Cannaceae
x 2.5
CANNA
flaccida
Zingiberaceae
x 6.5
AMOMUM
melegueta
Marantaceae
x 2
THALIA
dealbata

PLATE 16

LINEAR

Sparganiaceae—*Sparganium* (7 sp.) *eurycarpum* Engelm.; row I, 1.

Pontederiaceae—Embryos in this family are unique (except that Amomum in the Zingiberaceae is similar) in having extension to both poles of the seed.

Eichhornia (2 sp.) *crassipes* (Mart.) Solms; row I, 3.
Heteranthera (3 sp.) *dubia* (Jacq.) MacM.; row I, 4.
Pontederia cordata L.; row I, 2.

Typhaceae—*Typha* (2 sp.) *latifolia* L.; row II, 4.—The designation "copious," commonly aplied to the endosperm of this genus, seems inappropriate.

Araceae—The genera of this family lacking endosperm are difficult to classify and are not typically Linear but the endospermous members fit the Linear classification well.

Acorus calamus L.; row II, 3.
Arisaema (2 sp.) *triphyllum* (L.) Schott; row II, 1.
Calla palustris L.; row II, 2.
**Lysichiton*, **Orontium*, **Peltandra*, **Symplocarpus*.

Bromeliaceae—*Tillandsia* (3 sp.) *fasciculata* Sw., *usneoides* (L.) Raf.—This genus presents a unique form of embryo arrangement—one that is not characteristically Linear nor any other designated type. It would hardly be justified to recognize a special type for a single genus so Tillandsia has been included tentatively in the Linear group. Conceivably it could be regarded as an advanced form of the Broad type. The two species illustrated show considerable difference in embryo development and they are sometimes classed in two separate genera.

*Alismaceae—**Alisma* (2 sp.), **Damasonium*, **Echinodorus* (2 sp.), **Lophotocarpus*, **Sagittaria* (18 sp.).
*Butomaceae—**Butomus*.
*Hydrocharitaceae—**Anarchis*, **Limnobium*, **Vallisneria*.
*Juncaginaceae—**Scheuchzeria*, **Triglochin* (3 sp.).
*Naiadaceae—**Naias* (5 sp.).
*Potamogetonaceae — **Potamogeton* (29 sp.), **Ruppia*, **Zannichellia*, **Zostera*.

SUPPLEMENT; LINEAR GENERA (MONOCOTYLEDONES) IN NON-LINEAR FAMILIES

Cyperaceae (Capitate)—*Dulichium*, *Kyllinga*.

Smilacaceae (Rudimentary), *Smilax*.

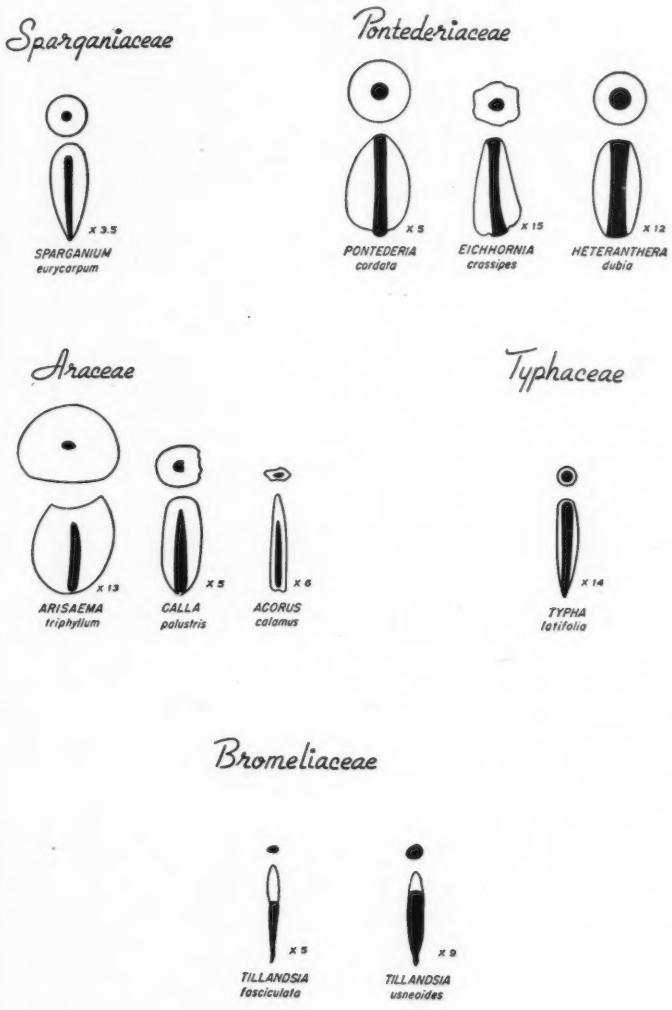
MICRO

The two following families are to the Monocots what the Monotropaceae and Pyrolaceae are to the Dicots. Unlike the latter families, however, the two Monocot families have no apparent intermediate links to other seed types. In the Burmanniaceae and Orchidaceae the embryo appears to be total though undifferentiated into distinct parts.

*Burmanniaceae—**Apteria*.

*Orchidaceae—Seeds of this family are commonly appendaged as is also the case with seeds of the Micro Dicots, the Monotropaceae and Pyrolaceae.
**Aplectrum*, **Corallorrhiza* (2 sp.), **Cypripedium*, **Epidendrum*, **Epipactis* (2 sp.), **Habenaria* (3 sp.), **Liparis* (2 sp.), **Spiranthes*, **Tipularia*.

PLATE 16

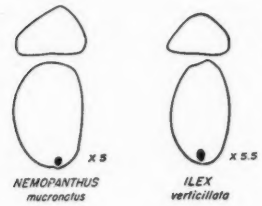

Sparganiaceae
X 3.5
SPARGANIUM
eurycarpum
Pontederiaceae
X 5
PONTEDERIA
cordata
X 15
EICHHORNIA
crassipes
X 12
HETERANTHERA
dubia
Araceae
X 13
ARISAEMA
triphyllum
X 5
CALLA
palustris
X 6
ACORUS
calamus
Typhaceae
X 14
TYPHA
latifolia
Bromeliaceae
X 5
TILLANDSIA
fasciculata
X 9
TILLANDSIA
usneoides

Dicotyledones

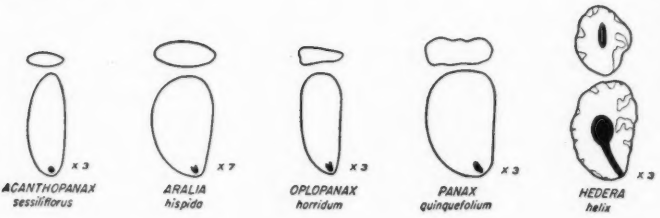
PLATE 17

RUDIMENTARY

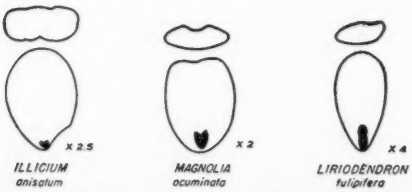
Aquifoliaceae



Araliaceae



Magnoliaceae



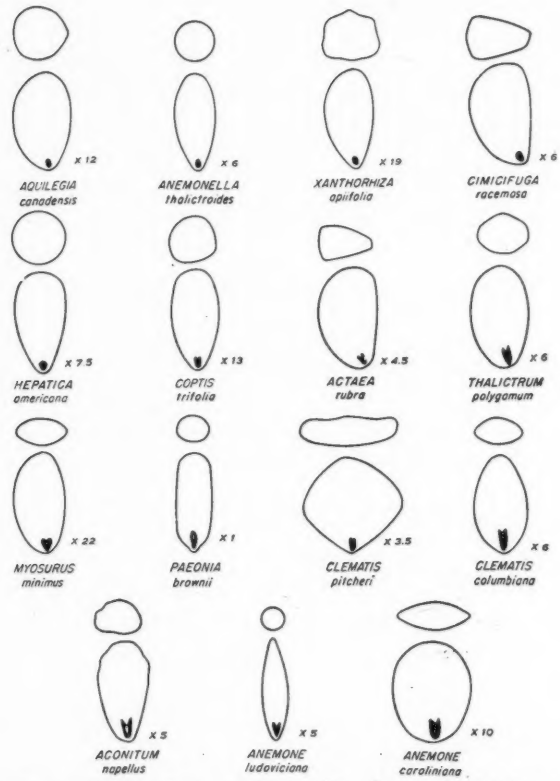
The three families illustrated on Plate 17 have their seeds in fleshy fruits; this may be mere coincidence, a view supported in some degree by the dry fruits of other families following. In all Rudimentary Dicots the endosperm is watery-fleshy or soft-fleshy.

Aquilfoliaceae—*Ilex* (16 sp.) *verticillata* (L.) Gray; row I, 2.
Nemopanthus mucronatus (L.) Trel.; row I, 1.
Araliaceae—*Acanthopanax sessiliflorus* Seem.; row II, 1.
Aralia (6 sp.) *hispida* Vent.; row II, 2.
Hedera helix L.; row II, 5. (SPATULATE).
Oplopanax (2 sp.) *horridum* (Sm.) Miquel; row II, 3.
Panax quinquefolium L.; row II, 4.
Magnoliaceae—*Illicium anisatum* L.; row III, 1.
Liriodendron tulipifera L.; row III, 3. (LINEAR).
Magnolia (6 sp.) *acuminata* L.; row III, 2.

PLATE 18

RUDIMENTARY

Ranunculaceae

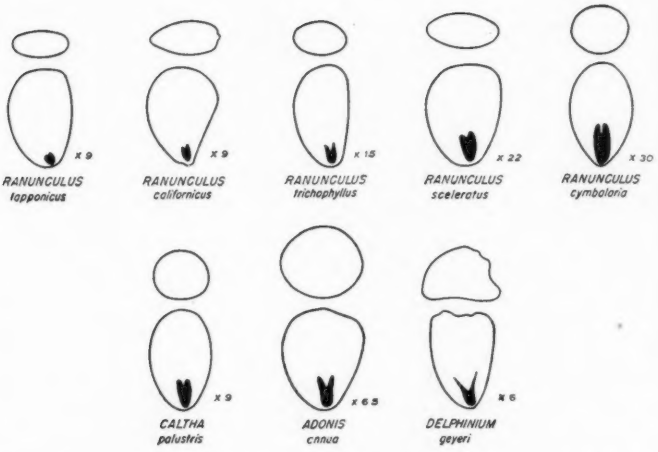


Ranunculaceae—This family is on the borderline between the Rudimentary and Linear types; its important genus Ranunculus (Plate 19) illustrates this fact. The endosperm is generally watery-fleshy.

Aconitum (3 sp.) *napellus* L.; row IV, 1.
Actaea (3 sp.) *rubra* (Ait.) Willd.; row II, 3.
Anemone (9 sp.); row IV, 2, 3. *Caroliniana* Walt., *ludoviciana* Nutt.—This latter species is often classed under Pulsatilla.
Anemonella thalictroides (L.) Spach.; row I, 2.
Aquilegia (6 sp.) *canadensis* L.; row I, 1.
Cimicifuga racemosa (L.) *Nutt.*; row I, 4.
Clematis (15 sp.); row III, 3, 4. *Columbiana* (Nutt.) Torr & Gray, *pitcheri* Torr. & Gray.
Coptis trifolia (L.) Salisb.; row II, 2.
Hepatica americana (DC.) Ker; row II, 1.
Myosurus minimus L.; row III, 1.
Paeonia (4 sp.) *brownii* Dougl.; row III, 2. (LINEAR).
Thalictrum (4 sp.) *polygamum* Muhl.; row II, 4.
Xanthorhiza apiifolia L'Her.; row I, 3.

RUDIMENTARY PLATE 19

Ranunculaceae concl.



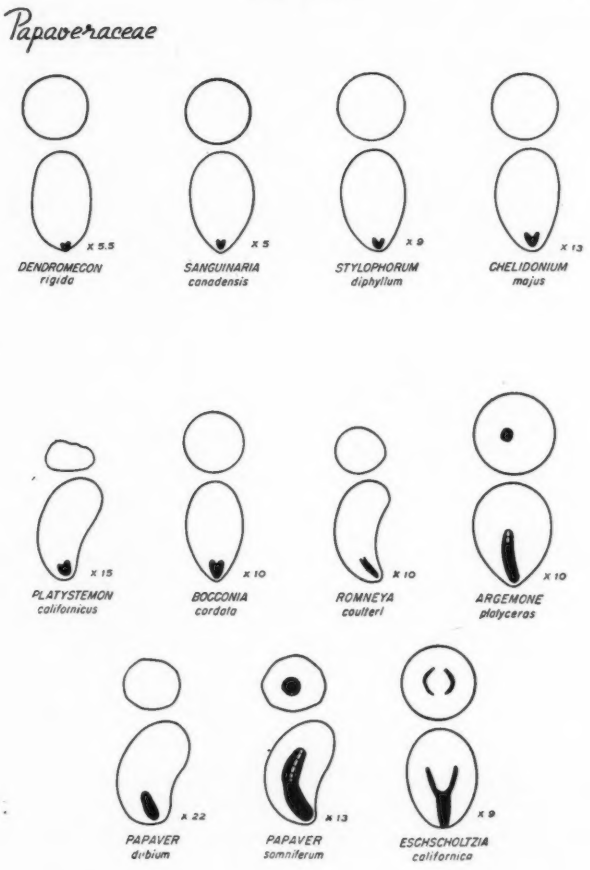
Ranunculaceae, concl.—*Adonis annua* L.; row II, 2.
Caltha palustris L.; row II, 1. (LINEAR).
Delphinium (11 sp.) *geyeri* Greene; row II, 3. (LINEAR). This species is average in embryo development for the genus; in *D. ajacis*, the cotyledons are considerably longer.
Ranunculus (23 sp.); row I, 1, 2, 3, 4, 5; *californicus* Benth. — This species is representative of a major part of the genus. — *Cymbalaria* Pursh (LINEAR), *lapponicus* L., *sceleratus* L. (LINEAR), *trichophyllus* Chaix (LINEAR).

PLATE 20

Papaveraceae—This family like the Ranunculaceae and Umbelliferae (Linear) shows obvious relationship to both the Rudimentary and Linear types.

Argemone (4 sp.) *platyceras* Link & Otto; row II, 4. (LINEAR).
Bocconia cordata Willd.; row II, 2.
Chelidonium majus L.; row I, 4.
Dendromecon rigida Benth.; row I, 1.
Eschscholtzia californica Cham.; row III, 3. (LINEAR).
Papaver (6 sp.); row III, 1, 2; *dubium* L., *somniferum* L. — Genus not uniform; *P. nudicaule* and *macounii* resemble *dubium* (relatively small embryo), *rhoeas* resembles *somniferum* (relatively large embryo) and *orientale* is intermediate.
Platystemon californicus Benth.; row II, 1.
Romneya coulteri Harv.; row II, 3. (LINEAR).
Sanguinaria canadensis L.; row I, 2.
Stylophorum diphyllum (Michx.) Nutt.; row I, 3.

RUDIMENTARY PLATE 20



SUPPLEMENT; RUDIMENTARY GENERA (DICOTYLEDONES) IN NON-RUDIMENTARY FAMILIES.

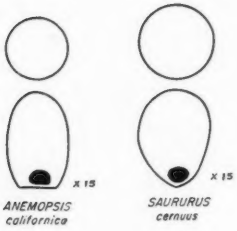
Berberidaceae (Linear)—*Achlys, Jeffersonia, Vancouveria.*

Oleaceae (Spatulate)—*Fraxinus quadrangulata* L.

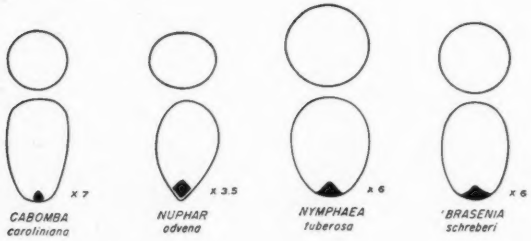
Umbelliferae (Linear)—*Aethusa, Centella, Cynosciadium, Erigenia, Heracleum, Hydrocotyle, Osmorrhiza, Sanicula Spermolepis, Trepocarpus.*

BROAD PLATE 21

Saururaceae



Nymphaeaceae



The embryos of the Broad Dicotyledones illustrated on Plate 21 are generally not as broad nor as large as those of Broad Monocots. However, they show resemblance in both embryo and endosperm. Seeds of both the Saururaceae and Nymphaeaceae (like the Cyperaceae and some genera of the Ranunculaceae, Papaveraceae, etc.) reveal rather clearly the outline of the embryo sac. The embryos of Anemopsis and Cabomba are intermediate between the Rudimentary and Broad types; their starchy endosperm is, however, characteristic of the Broad type.

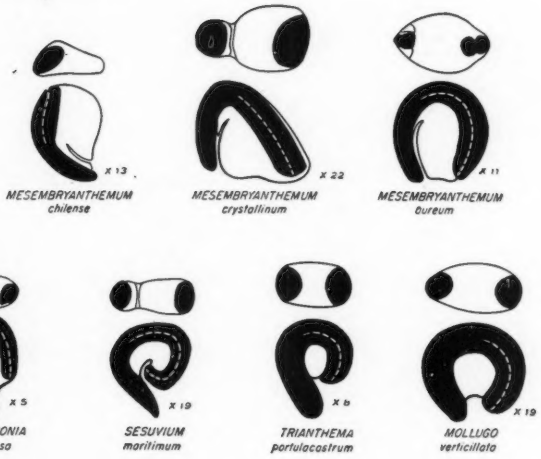
Saururaceae — *Anemopsis californica* (Nutt.) Hook. and Arn.; row I, 1.

Nymphaeaceae — *Brasenia schreberi* Gmel.; row II, 4.
Cabomba caroliniana Gray; row II, 1.
Nuphar (3 sp.) *advena* Ait.; row II, 2.
Saururus cernuus L.; row I, 2.
Nymphaea (3 sp.) *tuberosa* Paine; row II, 3.
**Nelumbo.*

PLATE 22A

PERIPHERAL

Aizoaceae



The "mealy" endosperm ascribed by floras to most Peripheral genera and families seems to be inappropriate; except for the Cactaceae and a few genera in other families, reasonably fresh seeds generally have a hard to horny, semi-translucent endosperm which nevertheless gives a definite starch reaction with iodine. Families within the Peripheral division are arranged in approximate order of the extent of expansion of their cotyledons.

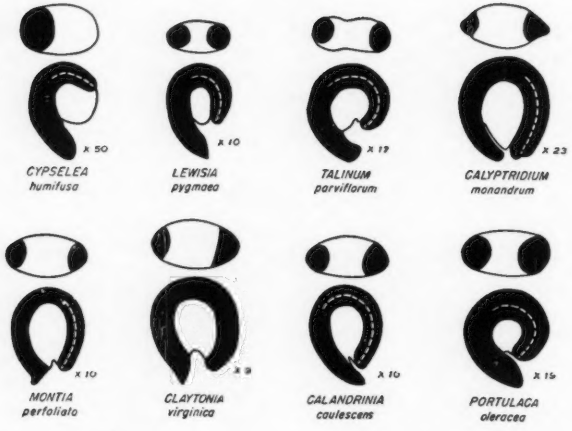
Aizoaceae—In Mesembryanthemum, Mollugo and Trianthema the endosperm is hard and semitransparent; in Sesuvium and Tetragonia it is soft and whitish.

Mesembryanthemum (4 sp.); row I.—By some botanists the three illustrated species, listed below, are classed in three separate genera; *aureum* L., *chilense* Molina, *crystallinum* L.

Mollugo (2 sp.) *verticillata* L.; row II, 4.
Sesuvium (3 sp.) *maritimum* (Walt.) B.S.P.; row II, 2.
Tetragonia expansa Murr.; row II, 1.
Trianthema portulacastrum L.; row II, 3.

PERIPHERAL PLATE 22B

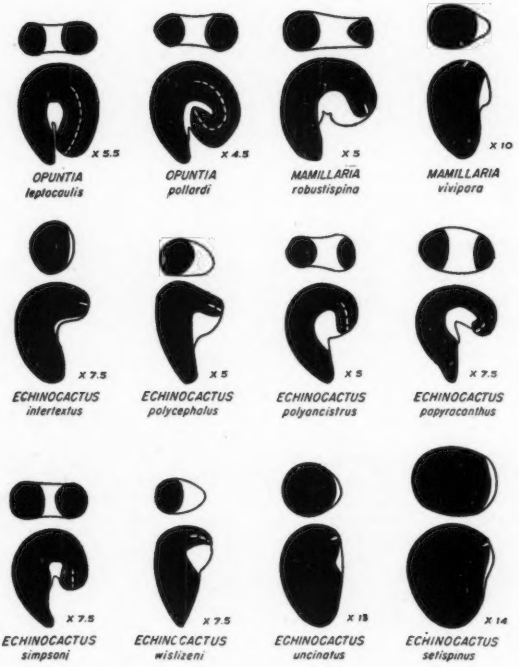
Portulacaceae



Portulacaceae—The endosperm is generally hard and semitransparent except for Talinum in which it is soft and whitish.

Calandrinia (3 sp.) *caulescens* H.B.K.; row II, 3.
Calyptridium (3 sp.) *monandrum* Nutt., row I, 4.
Claytonia (2 sp.), *virginica* L.; row II, 2.—C. *sarmentosa* differs in having two normal cotyledons instead of one.
Cypselea humifusa Turp.; row I, 1.
Lewisia (2 sp.) *pygmaea* (Gray) Rob.; row I, 2.
Montia (3 sp.) *perfoliata* (Donn.) Howell; row II, 1.
Portulaca (7 sp.) *oleracea* L.; row II, 4.
Talinum (5 sp.) *parviflorum* Nutt.; row I, 3.

Cactaceae



Cactaceae—The proper relative position of this family and, for that matter, of others in the Peripheral group, is difficult to ascertain and is necessarily speculative. Also the sequence of generic positions within the family is tentative. Nomenclature in the group has been complicated by divergent taxonomic concepts; the names used here represent conservative treatment. Endosperm, when present, is generally floury-starchy. In this family the embryo stalk, rather than the cotyledons, is usually expanded.

Echinocactus (21 sp.); rows II and III. Several species of the twenty-one studied in this complex genus are without endosperm; *intertextus* Engelm., *papyracanthus* Engelm,. *polyancistrus* Engelm. & Bigel., *polycephalus* Engelm. & Bigel., *setispinus* Engelm., *simpsoni* Engelm., *uncinatus* Gal., *wislizeni* Engelm.

Mamillaria (3 sp.); row I, 3, 4. This genus shows diversity in the two species illustrated; *robustispina* Schott, *vivipara* (Nutt.) Haw., *M. micromeris* lacks evident endosperm.

Opuntia (7 sp.); row I, 1, 2; *leptocaulis* DC., *pollardi* Britt. & Rose.—*O. imbricata* resembles *leptocaulis* but other species checked are like *pollardi*.

**Ariocarpus*, **Cereus* (3 sp.), **Echinocereus* (8 sp.).

PERIPHERAL PLATE 24

Caryophyllaceae—The genera illustrated on the bottom row of Plate 24 show inclination toward expanded cotyledons. Endosperm in this family is usually firm or hard and semitranslucent except in Agrostemma and Honckenya in which it is white and soft.

Agrostemma githago L.; row IV, 2.

Arenaria (6 sp.) *serpyllifolia* L.; row II, 3.

Cerastium (6 sp.) *viscosum* L.; row IV, 4.

Dianthus (7 sp.) *armeria* L.; row I, 4.

Gypsophila (2 sp.) *paniculata* L.; row III, 2.

Herniaria cinerea DC.; row I, 2.

Honckenya peploides Ehrh.; row II, 4. This plant is unique, not only in the family but also in the Peripheral division in having endosperm between the embryo and testa though *Mesembryanthemum crystallinum* (Pl. 22) shows a slight inclination in the same direction.

Lychnis (8 sp); row II, 1, 2; *alba* Mill., *apetala* L. — Two species resemble *apetala* and four *alba*.

Sagina (2 sp.) *linnaei* Presl; row I, 1.

Saponaria (3 sp.); row III, 4 and IV, 1; *officinalis* L., *vaccaria* L.

Silene (12 sp.) *latifolia* (Mill.) Britt. & Rendle; row III, 1. In *S. acaulis* and *tenax* the embryo is less arched, approximately as in *Lychnis apetala*.

Spergula (2 sp.) *arvensis* L.; row III, 3.

Spergularia (3 sp.) *salina* J. & C. Presl; row I, 3.

Stellaria (5 sp.) *media* (L.) Cyr.; row IV, 3. Genus reasonably uniform except for *S. borealis* which has less endosperm and a slightly coiled embryo.

PLATE 24

Caryophyllaceae

PERIPHERAL PLATE 25

Chenopodiaceae—Endosperm in genera of this family is usually firm to flinty and glass-like to whitish.

Allenrolfea occidentalis (Wats.) Kuntze; row II, 1.

Atriplex (33 sp.) *rosea* L.; row III, 5.

Axyris amaranthoides L.; row III, 1, 2. The two forms of seeds illustrated are not mentioned in floras. The two forms were obtained from the same plant and they differ as follows:—(1) Terminally winged, body elliptic, angled; surface flecked with small gray areas; (2) Not winged; body oval, lenticular; satiny dark gray. About one-sixth of the seeds are of this form.

Beta vulgaris L.; row IV, 1.

Chenopodium (22 sp.); row I; *album* L., *ambrosioides* L., *capitatum* L., *incisum* Poir.—Of the twenty-two species studied fourteen are like *C. album*, four like *ambrosioides*, one of the *capitatum* type and three like *incisum*. *C. capitatum* is sometimes classed in a separate genus.

Corispermum (3 sp.) *hyssopifolium* L.; row II, 4.

Cycloloma atriplicifolium (Spreng.) Coult.; row II, 3.

Eurotia lanata (Pursh) Moq.; row IV, 2.

Grayia spinosa (Hook.) Moq.; row III, 4.

Kochia (2 sp.) *scoparia* (L.) Schrad.; row IV, 3. This genus resembles Eurotia and Sarcobatus in greenish color of the cotyledons.

Monolepis (2 sp.) *nuttalliana* (Roem. & Schult.) Greene; row II, 2.

Spinacia oleracea L.; row IV, 4.

Suaeda (4 sp.) *depressa* (Pursh) Wats.; row V.

Suckleya suckleyana (Torr.) Rydb.; row III, 3.

**Salicornia* (4 sp.); **Salsola*, **Sarcobatus*.

PLATE 25

Chenopodiaceae

PERIPHERAL PLATE 26

Frankeniaceae—*Frankenia grandifolia* Cham. & Schlecht.; row I, 1. Seeds of this genus are characteristically Peripheral in having an embryo continuous with the periphery and in having starchy endosperm. Though curved embryos are typical of most Peripheral seeds, Frankenia has erect counterparts in Dianthus, Petiveria, Pisonia and several genera of the Polygonaceae.

Scleranthaceae—The endosperm is usually hard and translucent.

Anychia (2 sp.) *polygonoides* Raf.; row I, 2.

Paronychia jamesii Torr. & Gray; row I, 3.

Scleranthus annuus L.; row I, 4.

Amaranthaceae—In all genera of the family the cotyledons are at least slightly expanded. The endosperm varies from hard and translucent to granular and whitish.

Acanthochiton wrightii Torr.; row II, 2.

Acnida (4 sp.) *tamariscina* (Nutt.) Wood; row II, 3.

Amaranthus (10 sp.) *retroflexus* L.; row II, 1.

Centrostachys indica (L.) Standl.; row II, 6.

Froelichia campestris Small; row II, 4.

Gomphrena (5 sp.) *globosa* L.; row II, 5.

Phytolaccaceae—In Petiveria the endosperm is hard and semitransparent but in other genera it is soft or granular and whitish.

Petiveria alliacea L.; row III, 4. In this seed the thin cotyledons (not indicated in the diagram because of complexity) are folded convolutely about the upper half of the stalk.

Phaulothamnus spinescens Gray; row III, 2. Here as in certain Chenopodiaceae the cotyledon tips are greenish.

Phytolacca (2 sp.) *americana* L.; row III, 1.

Rivina humilis L.; row III, 3 .Resembles Petiveria, to some degree, in convolution of cotyledons.

PLATE 26

Frankeniaceae
Scleranthaceae
x 16
FRANKENIA grandifolia
x 22
ANYCHIA polygonoides
x 14
PARONYCHIA jamesii
x 10
SCLERANTHUS annuus
Amaranthaceae
x 14
AMARANTHUS retroflexus
x 13
ACANTHOCHITON wrightii
x 17
ACNIDA tamariscina
x 9
FROELICHIA campestris
x 9
GOMPHRENA globosa
x 4
CENTROSTACHYS indica
Phytolaccaceae
x 6
PHYTOLACCA americana
x 7.5
PHAULOTHAMNUS spinescens
x 7.5
RIVINA humilis
x 2
PETIVERIA alliacea

PERIPHERAL PLATE 27

Polygonaceae—The endosperm is hard and semitransparent, or occasionally crystalline-granular except in Brunnichia and Rheum in which it is whitish and soft to firm. Many genera in this family as well as in the Nyctaginaceae show resemblance to the Foliate subdivision in their expanded cotyledons as well as in erect, bent and folded arrangements.

Brunnichia cirrhosa Gaertn.; row III, 2.

Chorizanthe membranacea Benth.; row II, 5.

Coccolobis (2 sp.) *floridana* Meisn.; row III, 4. Rheum, Brunnichia and Coccolobis present a progressive series in rumination.

Eriogonum (6 sp.) *latifolium* Sm.; row II, 4.

Fagopyrum (2 sp.) *esculentum* Moench; row III, 5.

Oxyria digyna (L.) Hill; row III, 1.

Polygonella (2 sp.) *articulata* (L.) Meisn.; row I, 1.

Polygonum (37 sp.) rows I and II; *dumetorum* L., *pennsylvanicum* L., *punctatum* Ell., *sagittatum* L., *virginianum* L., *viviparum* L.—The section Tiniaria, represented by four species including *dumetorum*, is uniform; fifteen species in the section Avicularia are similar to Tiniaria and uniform; the section Persicaria (14 sp.) varies between the forms represented by *pennsylvanicum* and *punctatum;* in the section Echinocaulon, *P. arifolium* is similar to *sagittatum*.

Rheum rhaponticum L.; row III, 3.

Rumex (21 sp.) *crispus* L.; row I, 2. The genus is uniform except for two species, *R. verticillatus* and *maritimus*, in which the embryo is not strictly parietal and the plane of the cotyledons is at right angles to the wall instead of parallel to it.

Nyctaginaceae—The endosperm is usually crystalline-granular except in Mirabilis (whitish and mealy) and Pisonia (whitish and hard).

Abronia (4 sp.) *fragrans* Nutt.; row IV, 3. Only one cotyledon is developed, the other being rudimentary.

Allionia incarnata L.; row IV, 5. Inner cotyledon slightly smaller.

Boerhaavia (8 sp.) *torreyana* (Wats.) Standl.; row IV, 2.

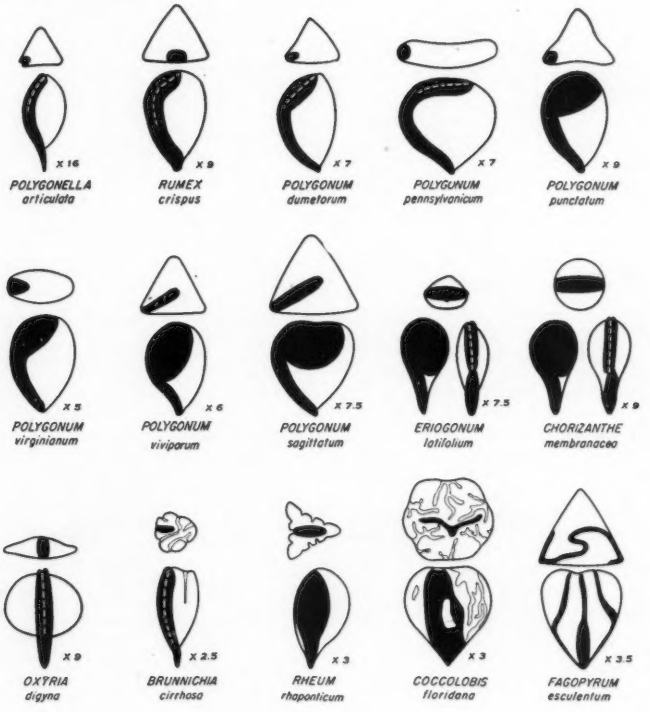
Mirabilis (2 sp.) *multiflora* (Torr.) Gray; row IV, 1. Inner cotyledon smaller.

Oxybaphus (4 sp.) *albidus* (Walt.) Sweet; row IV, 4.

Pisonia aculeata L.; row IV, 6. Distinctive in its short, straight, basal stalk; the inner cotyledon is smaller than the outer one.

PLATE 27

Polygonaceae



Nyctaginaceae

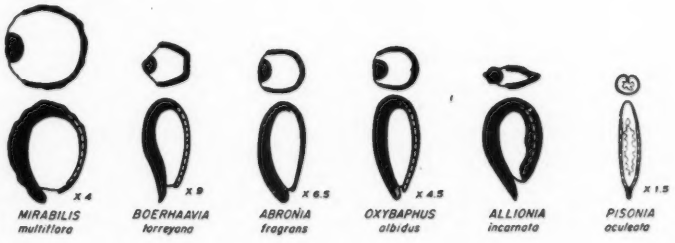


PLATE 28

LINEAR

Umbelliferae—Ten of the thirty-nine genera are classed as Rudimentary, five as Spatulate. The endosperm is usually firm but watery-fleshy.

Aethusa cynapium L.; row II, 4. (RUDIMENTARY).
Angelica (3 sp.) *villosa* (Walt.) B.S.P.; row III, 5.
Centella asiatica (L.) Urban; row I, 5. (RUDIMENTARY).
Chaerophyllum (2 sp.) *texanum* Coult. & Rose; row III, 2.
Coelopleurum (4 sp.) *maritimum* Coult. & Rose; row III, 4.
Cynosciadium pumilum (Engelm. & Gray) Coult. & Rose; row II, 5. (RUDIMENTARY).
Erigenia bulbosa Nutt.; row II, 1. (RUDIMENTARY).
Heracleum (3 sp.) *lanatum* Michx.; row I, 3. (RUDIMENTARY).
Hydrocotyle (4 sp.) *umbellata* L.; row I, 4. (RUDIMENTARY).
Leptotaenia (2 sp.) *eatoni* Coult. & Rose; row III, 1.
Ligusticum (2 sp.) *scothicum* L.; row IV, 1.
Lomatium (5 sp.) *macrocarpum* (Nutt.) Coult. & Rose; row IV, 4.
Osmorrhiza (4 sp.) *longistylis* (Torr.) DC.; row I, 2. (RUDIMENTARY).
Oxypolis (2 sp.) *rigidior* (L.) Raf.; row IV, 3.
Perideridia americana (Nutt.) Reichenb.; row IV, 2.
Ptilimnium (2 sp.) *laciniatum* (Engelm. & Gray) Kuntze; row III, 3.
Sanicula (3 sp.) *marilandica* L.; row II, 3. (RUDIMENTARY).
Spermolepis divaricata (Walt.) Raf.; row II, 2. (RUDIMENTARY).
Thaspium (2 sp.) *barbinode* (Michx.) Nutt.; row IV, 5.
Trepocarpus aethusae Nutt.; row I, 1. (RUDIMENTARY).

(Umbelliferae continued on plate 29)

PLATE 28

Umbelliferae

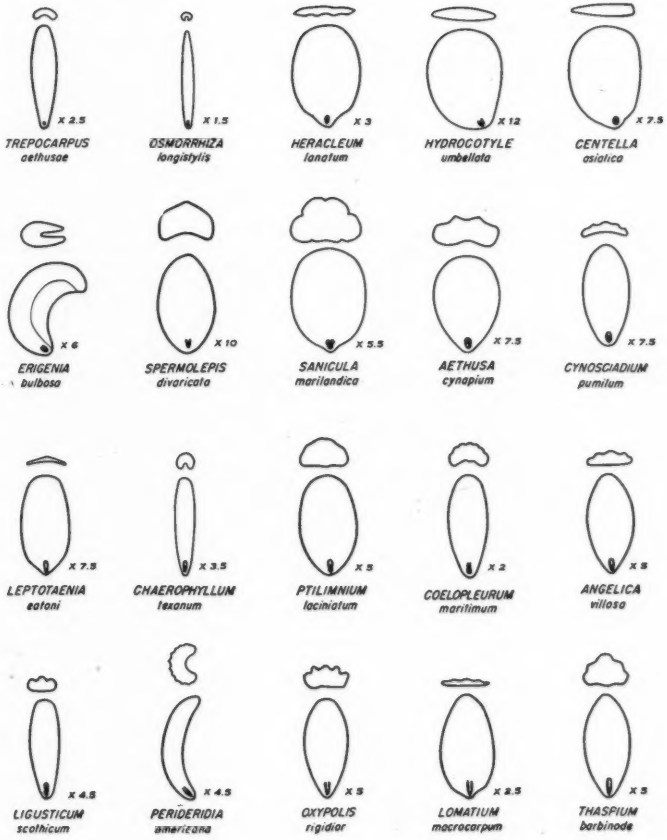


PLATE 29

LINEAR

Umbelliferae, concl.—

Anethum graveolens L.; row II, 1.

Apium graveolens L.; row III, 4.

Bifora americana (DC.) Wats.; row III, 3. This species is not stable in length of embryo.

Bowlesia septentrionalis Coult. & Rose; row III, 5. (SPATULATE).

Carum carvi L.; row III, 2.

Cicuta (6 sp.) *maculata* L.; row II, 4.

Conium (2 sp.) *maculatum* L.; row I, 4.

Coriandrum sativum L.; row IV, 2. (SPATULATE).

Cryptotaenia (4 sp.) *canadensis* (L.) DC.; row III, 1.

Cuminum cyminum L.; row I, 1.

Daucus (2 sp.) *carota* L.; row II, 3.

Eryngium (6 sp.) row I, 2, 3; *aquaticum* L., *articulatum* Hook. — The latter species is distinct from others in embryo length.

Foeniculum vulgare (L.) Gärtn.; row IV, 3. (SPATULATE).

Oenanthe sarmentosa Presl; row II, 2.

Pastinaca (3 sp.) *sativa* L.; row I, 5.

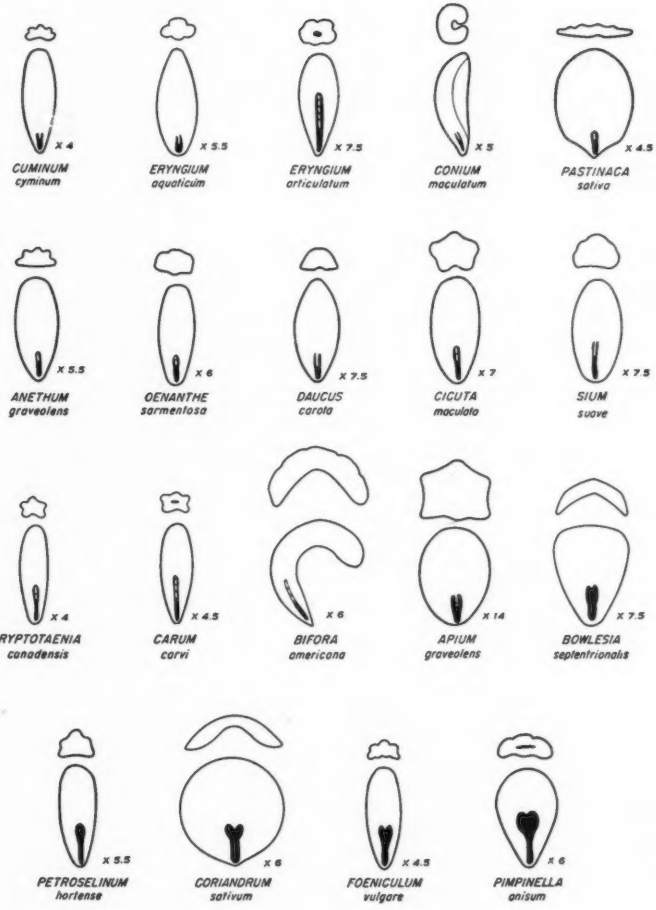
Petroselinum hortense Hoffm.; row IV, 1. (SPATULATE).

Pimpinella anisum L.; row IV, 4. (SPATULATE).

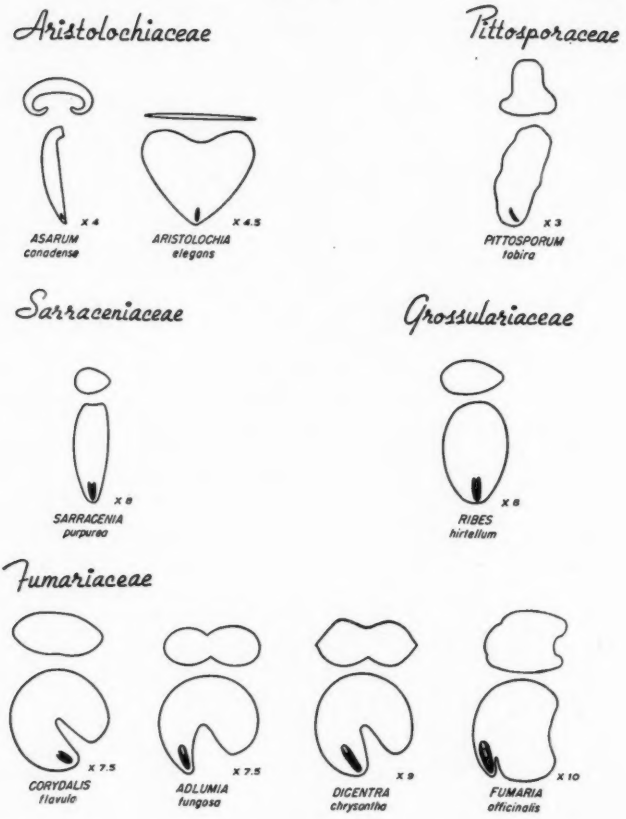
Sium suave Walt.; row II, 5. Embryo variable in length.

PLATE 29

Umbelliferae - Concl.



LINEAR PLATE 30



The endosperm in families listed on this plate is firm-fleshy with the exception of the Fumariaceae which has endosperm that is soft watery-fleshy and the Sarraceniaceae in which it is soft fleshy.

Aristolochiaceae—*Aristolochia* (5 sp.) *elegans* Mast; row I, 2.

Asarum (3 sp.) *canadense* L.; row I, 1.

Pittosporaceae — *Pittosporum tobira* Ait.; row I, 3.

Sarraceniaceae — *Sarracenia* (3 sp.) *purpurea* L.; row II, 1.

Grossulariaceae—*Ribes* (20 sp.) *hirtellum Michx.*; row II, 2.

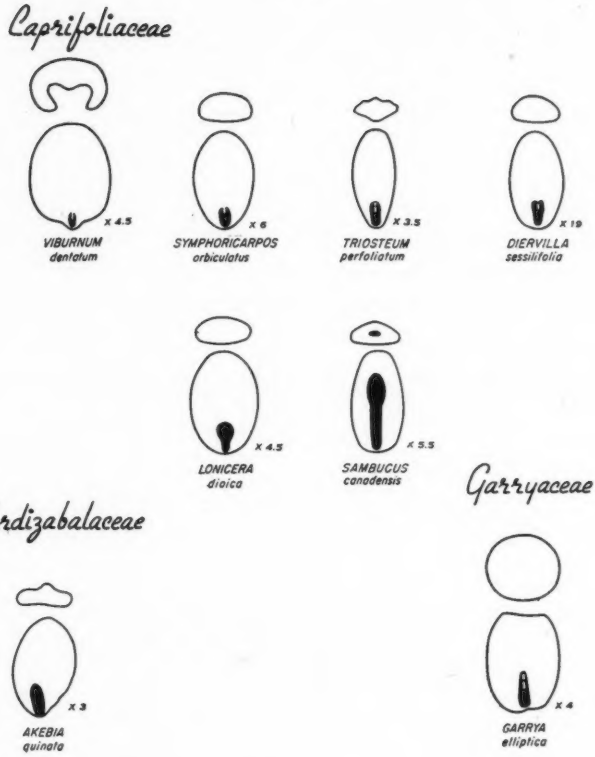
Fumariaceae — *Adlumia fungosa* (Ait.) Greene; row III, 2.

Corydalis (7 sp.) *flavula* (Raf.) DC.; row III, 1.

Dicentra (5 sp.) *chrysantha* (Hook. & Arn.) Walp.; row III, 3. *D. spectabilis* has a smaller embryo.

Fumaria officinalis L.; row III, 4.

LINEAR PLATE 31



Caprifoliaceae—The endosperm in all genera is soft and usually watery-fleshy except in Viburnum in which it is firm-fleshy.

Diervilla (3 sp.) *sessilifolia* Buckl.; row I, 4.

Lonicera (20 sp.) *dioica* L.; row II, 1. (SPATULATE). In *L. canadensis, oblongifolia, prolifera* and *xylosteum* the embryo is small compared to other species.

Sambucus (8 sp.) *canadensis* L.; row II, 2. (SPATULATE).

Symphoricarpos (6 sp.) *orbiculatus* Moench; row I, 2.

Triosteum (3 sp.) *perfoliatum* L.; row I, 3.

Viburnum (27 sp.) *dentatum* L.; row I, 1. Though seeds of the genus vary greatly in shape *V. dentatum* typifies reasonably well the embryo-endosperm relationship in all.

Lardizabalaceae — *Akebia quinata* Decne.; row III, 1. Embryo length not constant; endosperm firm-fleshy.

Garryaceae—*Garrya* (4 sp.) *elliptica* Dougl.; row III, 2. The endosperm is firm to hard.

PLATE 32

LINEAR

Anonaceae—Endosperm firm to hard, watery-fleshy.

Anona (2 sp.) *glabra* L.; row I, 2.

Asimina (3 sp.) *triloba* Dunal; row I, 1.

Buxaceae—Endosperm fleshy.

Buxus (2 sp.) *microphylla* Sieb. & Zucc.; row I, 4.

Pachysandra terminalis Sieb. & Zucc.; row I, 3.

**Simmondsia*, (INVESTING).

Santalaceae—Endosperm fleshy.

Buckleya distichophylla (Nutt.) Torr.; row II, 3. One cotyledon is about half the length of the other.

Comandra (3 sp.) *pallida* A. DC.; row II, 2.

Pyrularia pubera Michx.; row II, 1.

Loranthaceae—

Arceuthobium campylopodum Engelm.; row III, 1.

Phoradendron (4 sp.) sp.; row III, 2. This incompletely identified specimen was used because of its excellent condition; the endosperm in this family is succulent and inclines to shrivel rapidly.

Menyanthaceae—Endosperm fleshy.

Menyanthes trifoliata L.; row III, 3.

Nymphoides aquaticum (Walt.) Kuntze; row III, 4.

PLATE 32

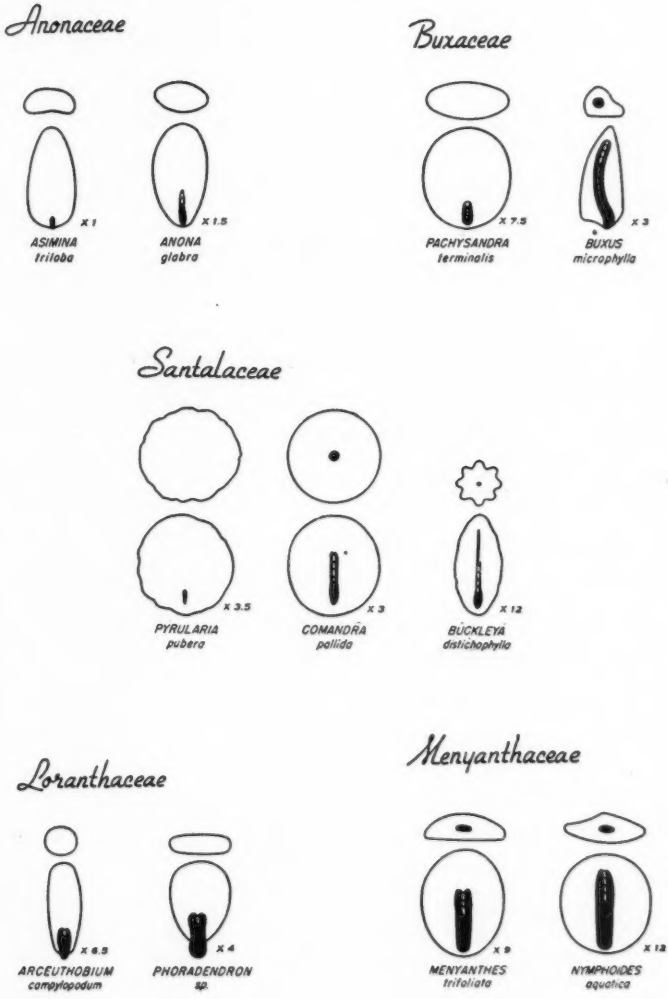

Anonaceae
Buxaceae
Santalaceae
Loranthaceae
Menyanthaceae
x 1
ASIMINA triloba
x 1.5
ANONA glabra
x 7.5
PACHYSANDRA terminalis
x 3
BUXUS microphylla
x 3.5
PYRULARIA pubera
x 3
COMANDRA pollida
x 12
BUCKLEYA distichophylla
x 6.5
ARCEUTHOBIUM campylopodum
x 4
PHORADENDRON sp.
x 9
MENYANTHES trifoliata
x 12
NYMPHOIDES aquatica

PLATE 33

LINEAR

Berberidaceae—The endosperm is fleshy except in Caulophyllum which is horny and has a terminal depression as in Thalia, Canna, etc. The family is quite diverse in its seeds.

Achlys triphylla (Smith) DC.; row I, 3. (RUDIMENTARY).

Berberis (18 sp.) *aquifolium* Pursh; row II, 4. (SPATULATE). The Odostemon section has a slightly larger embryo than the rest of the group.

Caulophyllum (4 sp.) *thalictroides* (L.) Michx.; row II, 1.

Diphylleia cymosa Michx.; row II, 3.

Jeffersonia diphylla (L.) Pers.; row I, 2. (RUDIMENTARY).

Nandina domestica Thunb.; row I, 4.

Podophyllum (2 sp.) *peltatum* L.; row II, 2.

Vancouveria hexandra (Hook.) Morr. & Decne.; row I, 1. (RUDIMENTARY).

Empetraceae—Endosperm soft-fleshy and watery.

Ceratiola ericoides Michx.; row III, 2.

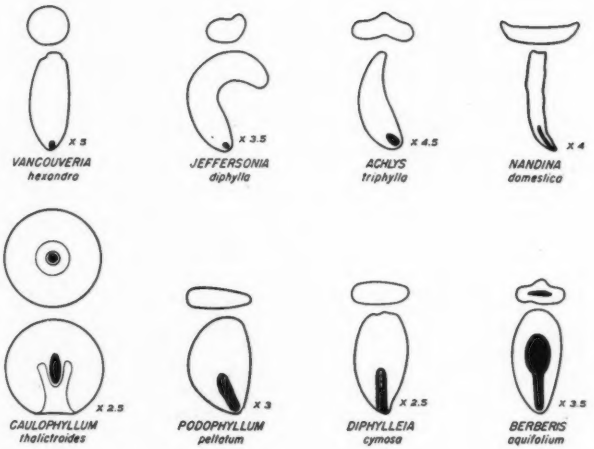
Empetrum nigrum L.; row III, 1.

Dilleniaceae—Endosperm soft-fleshy.

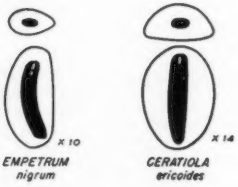
Actinidia (2 sp.) *polygama* Maxim.; row III, 3.

PLATE 33

Berberidaceae



Empetraceae



Dilleniaceae

PLATE 34

LINEAR

Vacciniaceae—Endosperm firm-fleshy.

Chiogenes hispidula (L.) Torr. & Gray; row I, 1.

Gaylussacia (4 sp.) *frondosa* (L.) Torr. & Gray; row I, 2.

Vaccinium (16 sp.) row I, 3, 4, 5; *angustifolium* Lam., *arboreum* Marsh., *macrocarpon* Ait.—*V. arboreum* appears to be representative of the Batodendron section, *macrocarpon* of Oxycoccus and *angustifolium* of the remainder.

Primulaceae—Endosperm hard or firm, semitransparent.

Anagallis arvensis L.; row II, 3.

Androsace (2 sp.) *septentrionalis* L.; row II, 4.

Dodecatheon (2 sp) *meadia* L.; row III, 2. (DWARF).

Glaux maritima L.; row III, 1.

Lysimachia (3 sp.) *terrestris* (L.) B.S.P.; row II, 5.

Primula (4 sp.) *eximia* Greene; row III, 3. (DWARF).

Samolus floribundus H.B.K.; row III, 4. (DWARF).

Steironema (3 sp.) *ciliatum* (L.) Raf.; row II, 2.

Trientalis americana (Pers.) Pursh; row II, 1.

Haloragidaceae—Endosperm soft-fleshy. The valved arrangement of fruits in this family is suggestive of the peculiar structure in Potamogeton.

Hippuris vulgaris L.; row IV, 3.

Myriophyllum (5 sp.) *spicatum* (Vaill.) L.; row IV, 2.

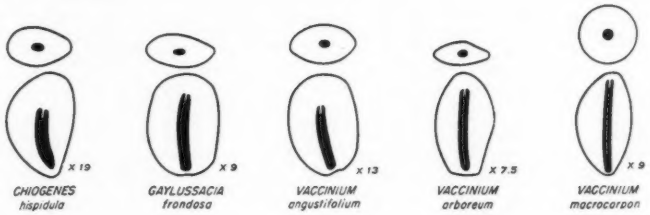
Proserpinaca pectinata Lam.; row IV, 1.

Platanaceae—The endosperm is a thin, fleshy external layer.

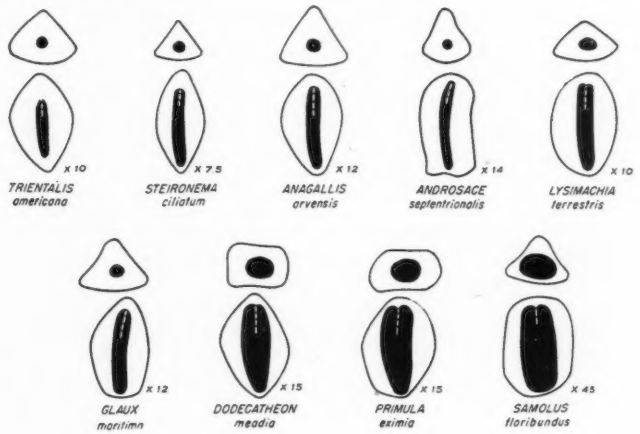
Platanus (4 sp.) *occidentalis* L.; row IV, 4.

PLATE 34

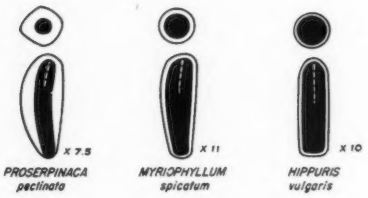
Vacciniaceae



Primulaceae



Haloragidaceae



Platanaceae

PLATE 35

LINEAR

In the Myrsinaceae the endosperm is hard but in all other families included in plate 35 it is fleshy.

Myrsinaceae—Endosperm hard, semitransparent.

Ardisia (3 sp.) *paniculata* Nutt.; row I, 1. *A. crenulata* and *japonica* are poly-embryoed.

Rapanea guianensis Aubl.; row I, 2.

Callitrichaceae — *Callitriche* (4 sp.) *autumnalis* L.; row I, 3.

Resedaceae—*Reseda odorata* L.; row I, 4.

Menispermaceae—

Calycocarpum (not illustrated; material too scant.) (SPATULATE).

Cocculus (2 sp.) *carolinus* (L.) DC.; row II, 2.

Menispermum (2 sp.) *canadense* (Tourn.) L.; row II, 1.

Koeberliniaceae—*Koeberlinia spinosa* Zucc.; row II, 3.

Capparidaceae—This family (mistakenly described in floras as having no endosperm) as well as other families listed on this page shows some resemblance to members of the Peripheral type. There are, however differences that appear important. Externally as well as internally the seeds of this family show strong resemblance to Koeberlinia to which, it is commonly assumed, there is no close relationship, whereas the seeds of the Cruciferae, a family supposedly closely related to the Capparidaceae, are very distinct.

Cleome (3 sp.); row III, 3, 4; *serrulata* Pursh, *spinosa* L., *C. lutea* resembles *serrulata*.

Cristatella jamesii Torr. & Gray; row III, 1.

Polanisia (2 sp.) *graveolens* Raf.; row III, 2.

Wislizenia refracta Engelm.; row III, 5.

PLATE 35

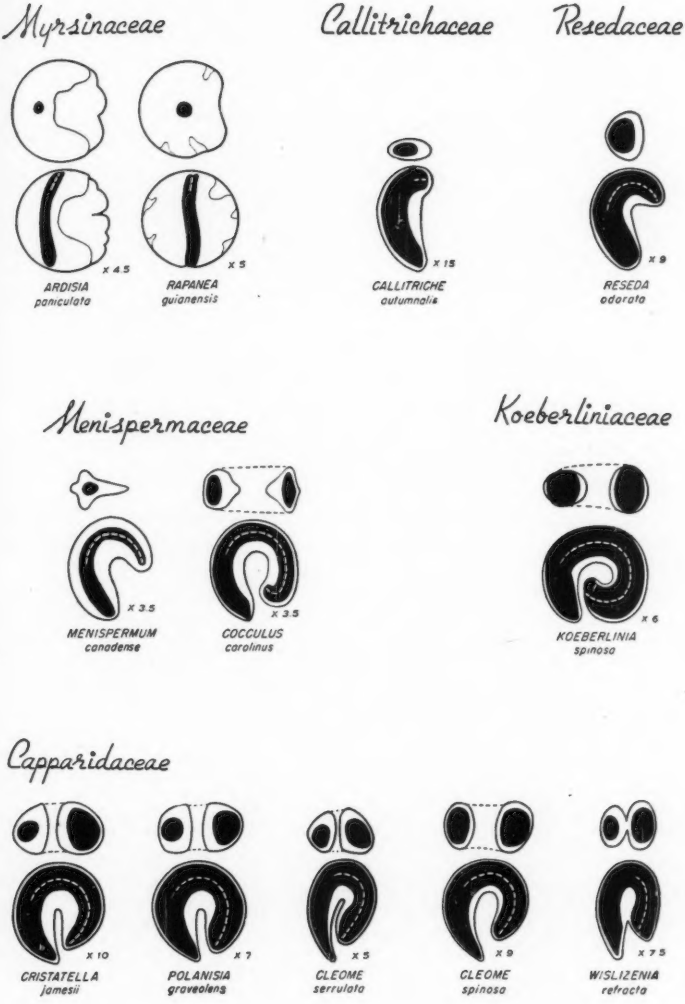

Myrsinaceae
Callitrichaceae
Resedaceae
x 4.5
x 5
x 15
x 9
ARDISIA paniculata
RAPANEA guianensis
CALLITRICHE autumnalis
RESEDA odorata
Menispermaceae
Koeberliniaceae
x 3.5
x 3.5
x 6
MENISPERMUM canadense
COCCULUS carolinus
KOEBERLINIA spinosa
Capparidaceae
x 10
x 7
x 5
x 9
x 7.5
CRISTATELLA jamesii
POLANISIA graveolens
CLEOME serrulata
CLEOME spinosa
WISLIZENIA refracta

PLATE 36

LINEAR

Solanaceae—Except for the two Dwarf genera the family is uniform in possessing a curved linear embryo. The endosperm is fleshy and semitransparent.

Atropa belladonna L.; row I, 2.
Capsicum (2 sp.) *baccatum* L.; row I, 1.
Datura (3 sp.) *stramonium* L.; row III, 2.
Hyoscyamus niger L.; row III, 3.
Lycium (8 sp.) *carolinianum* Walt.; row I, 3.
Lycopersicon (2 sp.) *esculentum* Mill.; row III, 4.
Nicandra physalodes (L.) Pers.; row III, 1.
Nicotiana (4 sp.); row IV, 2, 3; *attenuata* Torr., *glauca* Graham.—(DWARF). *N. bigelovii* is similar to *attenuata* and *tabacum* resembles *glauca*.
Petunia axillaris B.S.P.; row IV, 4. (DWARF).
Physalis (11 sp.); row I, 4; row II, 1. *heterophylla* Nees, *lobata* Torr. The species *lobata* is sometimes classed under another genus, Quincula.
Salpiglossis sinuata Ruiz & Pav.; row IV, 1.
Solanum (19 sp.) row II, 2, 3, 4. *dulcamara* L., *nigrum* L., *verbascifolium* L. Of the nineteen species studied, six fit the *dulcamara* group, ten *nigrum* and three *verbascifolium*.

*Casuarinaceae—**Casuarina*.

*Ceratophyllaceae—**Ceratophyllum*.—The outline of the embryo is not characteristically Linear but this is due to arching of the cotyledons over the large plumule. The cotyledons are not expanded.

*Combretaceae—**Psidium* (2 sp.). Whether by coincidence or not the valved seed coats of Psidium have a striking resemblance to the valved pericarp of Potamogeton fruits.

*Rhizophoraceae—**Rhizophora*.

SUPPLEMENT; LINEAR GENERA IN NON-LINEAR FAMILIES

Boraginaceae (Spatulate)—*Ehretia*.
Convolvulaceae (Folded)—*Cuscuta*.
Ericaceae (Dwarf). *Arctostaphylos* (in part), *Enkianthus*.
Euphorbiaceae (Spatulate)—*Reverchonia*.
Hydrophyllaceae (Spatulate)—*Hydrophyllum* (in part), *Phacelia* (in part).
Magnoliaceae (Rudimentary)—*Liriodendron*.
Papaveraceae (Rudimentary)—*Argemone*, *Eschscholtzia*, *Papaver*, *Romneya*.
Ranunculaceae (Rudimentary)—*Adonis*, *Anemone*, *Caltha*, *Clematis*, *Delphinium*. *Paeonia*, *Ranunculus* (in part).
Rubiaceae (Spatulate)—*Crusea*, *Galium* (in part).
Rutaceae (Spatulate)—*Cneoridium*, *Ruta*, *Thamnosma*.
Saxifragaceae (Dwarf)—*Philadelphus*.
Scrophulariaceae (Dwarf)—*Melampyrum*, *Pedicularis*.
*Myrtaceae (Folded)—**Myrtus*.

PLATE 36

Solanaceae

PLATE 37

DWARF

With the exception of Drosera (crystalline-granular) the endosperm in all Dwarf seeds is fleshy and generally soft-fleshy. In Polypremum and Lindernia it is firm-fleshy as is also the case in most of the Linear and Spatulate genera that occur in Dwarf families.

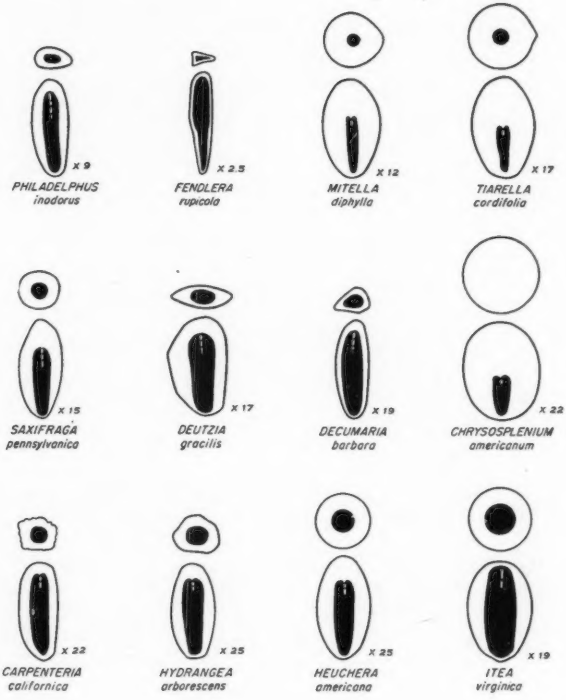
Saxifragaceae—

Carpenteria californica Torr.; row III, 1.
Chrysosplenium americanum Schwein.; row II, 4.
Decumaria barbara L.; row II, 3.
Deutzia (2 sp.) *gracilis* Sieb. & Zucc.; row II, 2.
Fendlera (2 sp.) *rupicola* Gray; row I, 2. (SPATULATE).
Heuchera (9 sp.) *americana* L.; row III, 3.
Hydrangea (3 sp.) *arborescens* L.; row III, 2.
Itea virginica L.; row III, 4.
Mitella diphylla L.; row I, 3.
Philadelphus (3 sp.) *inodorus* L.; row I, 1. (LINEAR).
Saxifraga (2 sp.) *pennsylvanica* L.; row II, 1.
Tiarella (2 sp.) *cordifolia* L.; row I, 4.

Clethraceae—*Clethra alnifolia* L.; row IV..

PLATE 37

Saxifragaceae



Clethraceae

PLATE 38

DWARF

Ericaceae—*Arbutus* (3 sp.) *menziesii* Pursh; row I, 5. (SPATULATE).

Arctostaphylos (15 sp.); row I, 1, 2, 3,4; *alpina* (L.) Spreng. (LINEAR), *andersonii* Gray (LINEAR), *bicolor* (Nutt.) Gray (SPATULATE), *uva-ursi* Spreng. (LINEAR).—*A. alpina* and *bicolor* are distinct among species in the seed collection; there are five species of the *uva-ursi* form and eight similar to *andersonii*.

Cassiope hypnoides (L.) D. Don; row IV, 4.

Chamaedaphne calyculata (L.) Moench; row III, 4.

Enkianthus perulatus Schneid.; row II, 1. (LINEAR).

Epigaea repens L.; row IV, 1.

Gaultheria (3 sp.) *shallon* Pursh; row III, 3.

Kalmia (2 sp.) *latifolia* L.; row II, 5.

Leiophyllum buxifolium (Berg.) Ell.; row IV, 5.

Leucothoe (4 sp.) *racemosa* (L.) Gray; row III, 5.

Lyonia (5 sp.); row IV, 2, 3; *ligustrina* (L.) DC., *nitida* (Bartr.) Fern.

Menziesia pilosa (Michx.) Pers.; row II, 4.

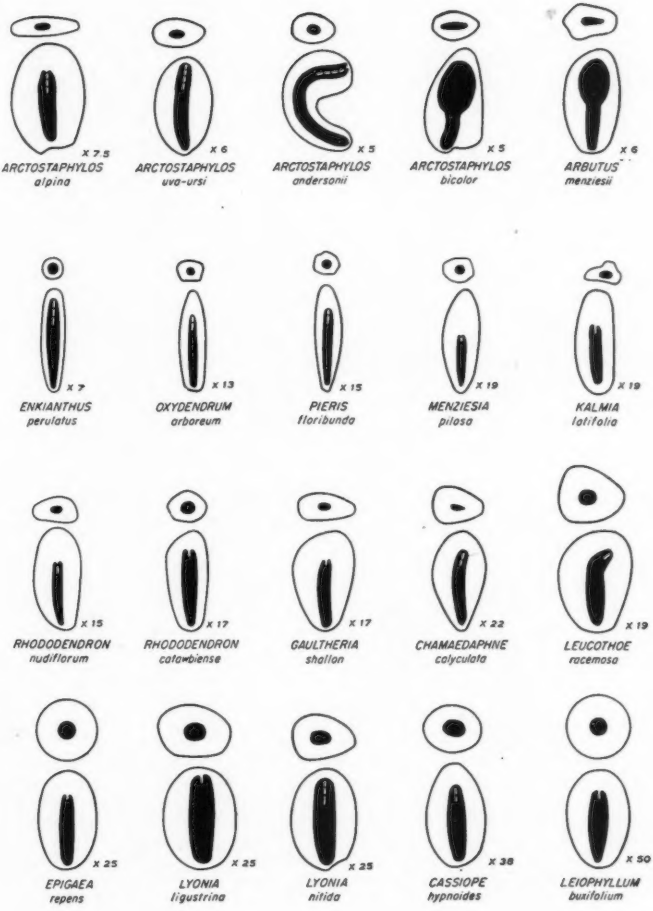
Oxydendrum arboreum (L.) DC.; row II, 2.

Pieris floribunda (Pursh) Benth.; row II, 3.

Rhododendron (22 sp.); row III, 1, 2; *catawbiense* Michx., *nudiflorum* (L.) Torr.

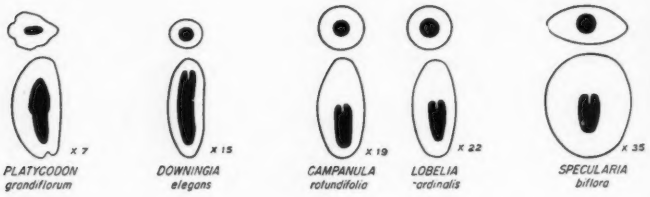
PLATE 38

Ericaceae

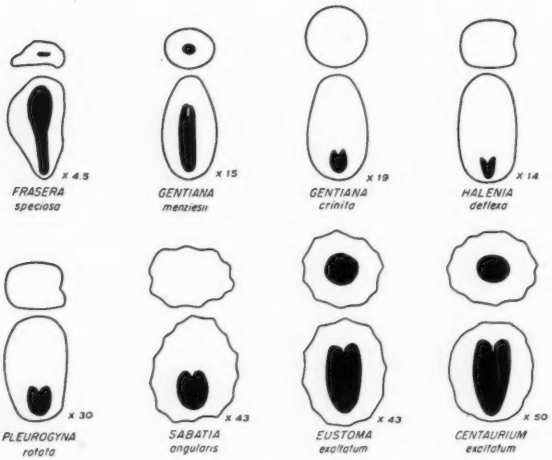


DWARF PLATE 39

Campanulaceae



Gentianaceae



Campanulaceae—*Campanula* (7 sp.) *rotundifolia* L.; row I, 3. *C. rapunculoides* and *C. medium* have somewhat larger embryos.

Downingia elegans (Dougl.) Greene; row I, 2.

Lobelia (8 sp.) *cardinalis* L.; row I, 4.

Platycodon grandiflorum A. DC.; row I, 1. (SPATULATE).

Specularia (2 sp.) *biflora* (Ruiz and Pav.) Fisch. & Meyer; row I, 5.

**Sphenoclea*. A negligible lining of endosperm is present.

Gentianaceae — *Centaurium exaltum* Griseb.) Wight; row III, 4.

Eustoma (2 sp.) *exaltatum* (L.) Griseb.; row III, 3.

Frasera speciosa Dougl.; row II, 1. (SPATULATE).

Gentiana (8 sp.); row II, 2, 3; *crinita* Froel., *menziesii* Griseb. *C. puberula* resembles *menziesii;* other species have shorter embryo.

Halenia deflexa (Sm.) Griseb.; row II, 4.

Pleurogyna rotata (L.) Griseb.; row III, 1.

Sabatia (2 sp.) *angularis* (L.) Pursh; row III, 2.

DWARF PLATE 40

Droseraceae

DROSERA
intermedia

Orobanchaceae

CONOPHOLIS
mexicana

EPIFAGUS
virginiana

Loganiaceae

GELSEMIUM
sempervirens

BUDDLEIA
racemosa

CYNOCTONUM
mitreola

POLYPREMUM
procumbens

Cephalotaceae

PARNASSIA
palustris

Penthoraceae

PENTHORUM
sedoides

Droseraceae — *Drosera* (3 sp.) *intermedia* Hayne; row I, 1. The genus is not very uniform; embryo relatively larger in *D. rotundifolia* (smaller seed) and smaller in *filiformis*.

Orobanchaceae — Internal anatomy in seeds of this family shows considerable resemblance to the Monotropaceae and Pyrolaceae of the Micro type.
Conopholis mexicana Gray; row I, 2.
Epifagus virginica (L.) Bart.; row I, 3.

Loganiaceae — *Buddleia racemosa* Torr.; row II, 2.
Cynoctonum mitreola (L.) Britton; row II, 3.
Gelsemium sempervirens (L.) Ait.; row II, 1. (SPATULATE).
Polypremum procumbens L.; row II, 4.

Cephalotaceae—*Parnassia* (3 sp.) *palustris* L. Fern.; row III, 1.

Penthoraceae — *Penthorum sedoides* L.; row III, 2.

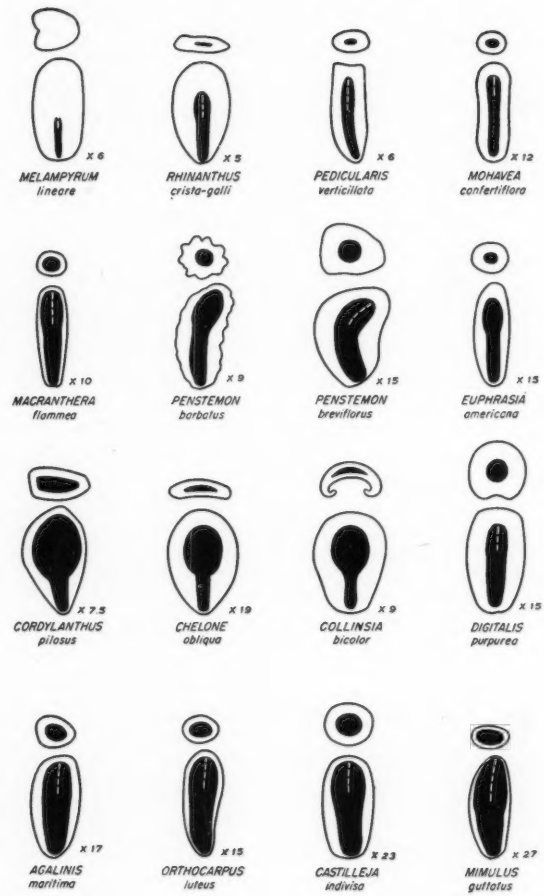
DWARF PLATE 41

Scrophulariaceae — *Agalinis* (6 sp.) *maritima* Raf.; row IV, 1.
Castilleja (14 sp.) *indivisa* Engelm.; row IV, 3.
Chelone (2 sp.) *obliqua* L.; row III, 2. (SPATULATE).
Collinsia (3 sp.) *bicolor* Benth.; row III, 3. (SPATULATE).
Cordylanthus (2 sp.) *pilosus* Gray; row III, 1. (SPATULATE).
Digitalis (2 sp.) *purpurea* L.; row III, 4.
Euphrasia americana Wettst.; row II, 4. (SPATULATE).
Macranthera flammea (Bartr.) Pennell; row II, 1. (SPATULATE).
Melampyrum lineare Lam.; row I, 1. (LINEAR).
Mimulus (5 sp.) *guttatus* DC.; row IV, 4.
Mohavea (2 sp.) *confertiflora* (Benth.) Pennell; row I, 4.
Orthocarpus (2 sp.) *luteus* Nutt.; row IV, 2.
Pedicularis (4 sp.) *verticillata* L.; row I, 3. (LINEAR).
Penstemon (25 sp.); row II, 2, 3; *barbatus* (Cav.) Roth, *breviflorus* Lindl. (SPATULATE). The genus is fairly uniform within the latitude indicated by the two illustrations.
Rhinanthus crista-galli L.; row I, 2. (SPATULATE).

(Scrophulariaceae continued on plate 42)

PLATE 41

Scrophulariaceae



DWARF PLATE 42

Scrophulariaceae—*Antirrhinum* (2 sp.) *coulterianum* Benth.; row II, 2.
Aureolaria (3 sp.) *virginica* (L.) Farw.; row I, 1. Considerable embryo variation occurs within this genus.
Bacopa (3 sp.) *acuminata* (Walt.) Robinson; row III, 2.
Conobea multifida (Michx.) Benth.; row IV, 1.
Gratiola (4 sp.) *virginiana* L.; row III, 4.
Limosella aquatica L.; row I, 4.

*Crassulaceae — **Sedum* (3 sp.) Endosperm is a negligible lining.

*Datiscaceae—**Datisca*.

*Elatinaceae—**Bergia*, **Elatine* (2 sp.)

*Hypericaceae — **Ascyrum* (4 sp.), **Hypericum* (21 sp.).

Linaria (3 sp.) *canadensis* (L.) Dumort.; row II, 3.
Lindernia (2 sp.) *dubia* (L.) Pennell; row III, 3.
Mazus japonicus Kuntze; row III, 1.
Paulownia tomentosa Steud.; row II, 4.
Scoparia dulcis L.; row IV, 2.
Scrophularia (4 sp.) *californica* Cham.; row I, 2.
Verbascum (2 sp.) *thapsus* L.; row I, 3.
Veronica (13 sp.) *anagallis-aquatica* L.; row II, 1.

*Melastomaceae—**Rhexia* (3 sp.) *R. alifanus* differs markedly from *virginica* and *mariana* both externally and internally; the latter two species are strongly arched.

*Podostemaceae—**Podostemum*.

SUPPLEMENT; DWARF GENERA IN NON-DWARF FAMILIES

Hydrophyllaceae (Spatulate)—*Eriodictyon, Hydrolea, Nama.*
Polemoniaceae (Spatulate)—*Navarretia.*
Primulaceae (Linear)—*Dodecatheon, Primula.*
Rubiaceae (Spatulate)—*Guettarda, Houstonia, Oldenlandia, Pentodon.*
Solanaceae (Linear)—*Nicotiana, Petunia.*

MICRO

This type represented by the two families below as well as by the Orchidaceae and Burmanniaceae is distinct in the following characters: minuteness of seed, the interior measuring 0.2 mm or less; reduction of tissues in seed interior to a small number of cells —approximately 25 to 100; comparatively undifferentiated state of the embryo and the tendency (with exceptions) to produce wings, tails or similar appendages on the surface. Certain botanical references indicate that endosperm is lacking in the Monotropaceae and Pyrolaceae but recent embryological work[2] has shown that endosperm is present in amounts that are moderate to considerable as compared to the embryo. No diagrams were prepared, however, since the embryo and endosperm are not readily distinguished.

Monotropaceae—*Monotropa, Pterospora.*

Pyrolaceae—*Chimaphila* (2 sp.), *Pyrola* (3 sp).

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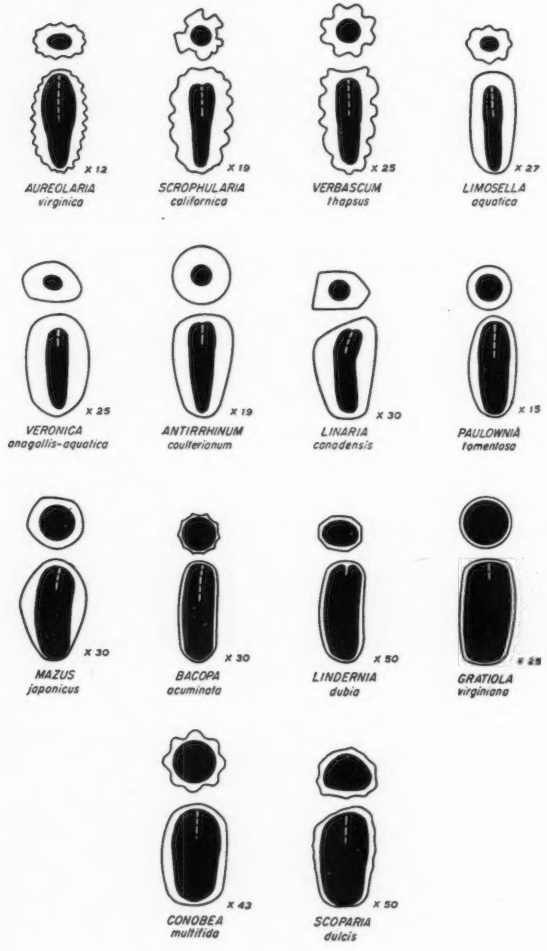
2 Copeland, Herbert F., The development of seeds in certain Ericales. Am. Jour. Bot. **20**(8):513-517, 1933. Also other papers by the same author.

PLATE 42

Scrophulariaceae Concl.



SPATULATE PLATE 43

Hydrophyllaceae—This borderline family combines Dwarf, Linear and Spatulate types; the genera Hydrophyllum and Phacelia have species representative of both Linear and Spatulate types. The endosperm is soft-fleshy in the Dwarf genera (as usual) and is fleshy or firm-fleshy in all others except *Hydrophyllum canadense* in which it is hard.

Ellisia nyctelea L.; row I, 4.

Emmenanthe penduliflora Benth.; row III, 1.

Eriodictyon (2 sp.) *angustifolium* Nutt.; row I, 1. (DWARF).

Hydrolea (2 sp.) *affinis* Gray; row I, 3. (DWARF).

Hydrophyllum (2 sp.); row II, 1, 2; *canadense* L. (LINEAR), *capitatum* Dougl.

Nama parryi (Gray) Greene; row I, 2. (DWARF).

Nemophila (2 sp.) *menziesii* Hook. & Arn.; row III, 2.

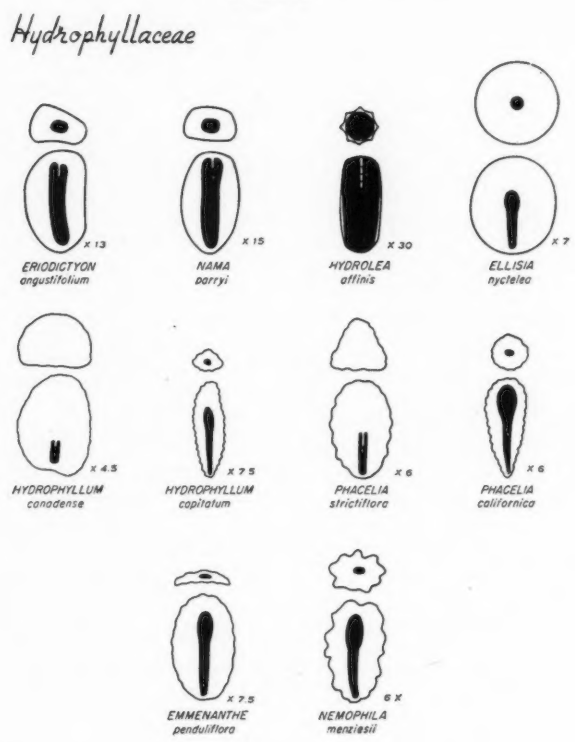
Phacelia (11 sp.); row II, 3, 4, *californica* Cham., *strictiflora* (Engelm. & Gray) Gray (LINEAR). *P. strictiflora* is unique among specimens studied in this genus; others resemble *californica* except that species with somewhat triangular seeds incline to have a larger, more broadly spatulate embryo.

Cyrillaceae—Endosperm fleshy. *Cyrilla racemiflora* L.; row IV, 1.

Zygophyllaceae—Endosperm hard (Larrea). *Larrea tridentata* (DC.) Cov.; row IV., 2. **Kallstroemia* (3 sp.) (INVESTING). **Tribulus* (2 sp).

Ebenaceae—Endosperm very hard. *Diospyros* (4 sp.) *virginiana* L.; row IV, 3.

PLATE 43


Hydrophyllaceae
x 13
ERIODICTYON angustifolium
x 15
NAMA parryi
x 30
HYDROLEA affinis
x 7
ELLISIA nyctelea
x 4.5
HYDROPHYLLUM canadense
x 7.5
HYDROPHYLLUM capitatum
x 6
PHACELIA strictiflora
x 6
PHACELIA californica
x 7.5
EMMENANTHE penduliflora
6 x
NEMOPHILA menziesii
Cyrillaceae
x 9
CYRILLA racemiflora
Zygophyllaceae
x 4.5
LARREA tridentata
Ebenaceae
x 1
DIOSPYROS virginiana

SPATULATE PLATE 44

Rubiaceae—Numerous genera in this family depict rudimentary development of the Spatulate type. Endosperm varies in the Dwarf genera from soft-fleshy to fleshy and in the others from firm to hard-fleshy.

Asperula odorata L.; row IV, 4.

Borreria (2 sp.) *ocimoides* (Burm.) DC.; row IV, 3.

Bouvardia glaberrima Engelm.; row III, 3.

Chiococca (2 sp.) *alba* (L.) A. Hitchc.; row III, 4.

Crusea tricocca (Torr. & Gray) Heller; row II, 1. (LINEAR).

Erithalis fruticosa L.; row IV, 2.

Galium (15 sp.); row II, 2, 3, 4; *bermudense* L. (LINEAR), *latifolium* Michx., *trifidum* L. (LINEAR). About half of the species are Linear and half Spatulate.

Guettarda (2 sp.) *elliptica* Sw.; row I, 4. (DWARF).

Houstonia (6 sp.) *caerulea* L.; row I, 1. (DWARF).

Mitchella repens L.; row III, 1.

Oldenlandia (2 sp.) *uniflora* L.; row I, 3. (DWARF).

Pentodon halei (Torr. & Gray) Gray; row I, 2. (DWARF).

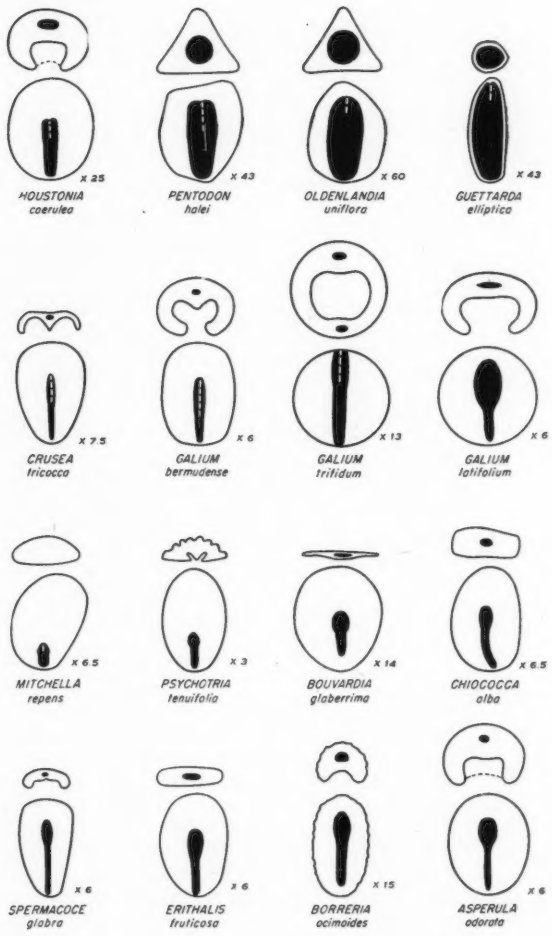
Psychotria (2 sp.) *tenuifolia* (Sw.); row III, 2.

Spermacoce glabra Michx.; row IV, 1.

(Rubiaceae continued on plate 45)

PLATE 44

Rubiaceae



SPATULATE PLATE 45

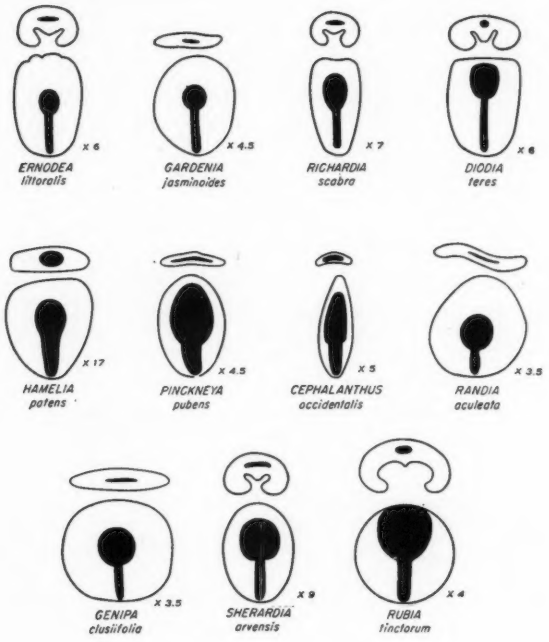
Rubiaceae, concl.
Cephalanthus occidentalis L.; row II, 3.
Diodia (2 sp.) *teres* Walt.; row I, 4.
Ernodea littoralis Sw.; row I, 1.
Gardenia jasminoides Ellis; row I, 2.
Genipa clusiifolia Jacq.; row III, 1.
Hamelia patens Jacq.; row II, 1.
Pinckneya pubens Michx.; row II, 2.
Randia (2 sp.) *aculeata* L.; row II, 4.
Richardia (2 sp.) *scabra* L.; row I, 3.
Rubia tinctorum L.; row III, 3.
Sherardia arvensis L.; row III, 2.

Vitaceae—The short-stalked Spatulate embryos of this family are unique except for Mitchella, Psychotria and Bouvardia in the Rubiaceae. The endosperm is firm watery-fleshy.

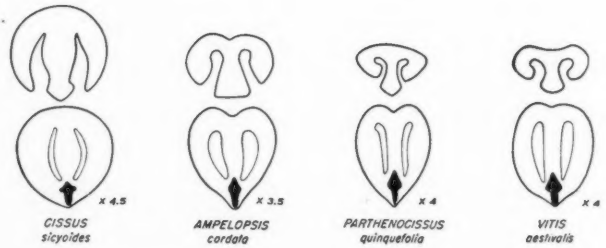
Ampelopsis (2 sp.) cordata Michx.; row IV, 2.
Cissus (2 sp.) *sicyoides* L.; row IV, 1.
Parthenocissus quinquefolia (L.) Planch.; row IV, 3.
Vitis (16 sp.) *aestivalis* Michx.; row IV, 4.

PLATE 45

Rubiaceae (cont.)



Vitaceae



SPATULATE PLATE 46

Plantaginaceae—*Plantago* (14 sp.) *rhodosperma* Decne.; row I, 1. The genus is fairly uniform internally though size and shape of seeds is diverse; some species like *P. arenaria* and *lanceolata* have embryos that are relatively slender. The endosperm is firm, transparent and waxy in appearance.

Plumbaginaceae—Endosperm is firm crystalline-granular.

Limonium (2 sp.) *californicum* (Boiss.) Heller; row I, 3.

Plumbago capensis Thunb.; row I, 2.

Loasaceae—Endosperm is soft-fleshy.

Mentzelia (5 sp.); row II, 1, 2; *decapetela* (Pursh) Urban & Gilg, *lindleyi* Torr. & Gray (BENT). *M. multiflora* and *stricta* resemble *decapetala; dispersa* is similar to *lindleyi.*

Cistaceae—Endosperm is hard and transparent; in Helianthemum it gives some starch reaction suggesting the Peripheral division.

Helianthemum (5 sp.) *canadense* (L.) Michx.; row II, 3. (BENT).

Lechea (4 sp.) *villosa.;* row II, 4.

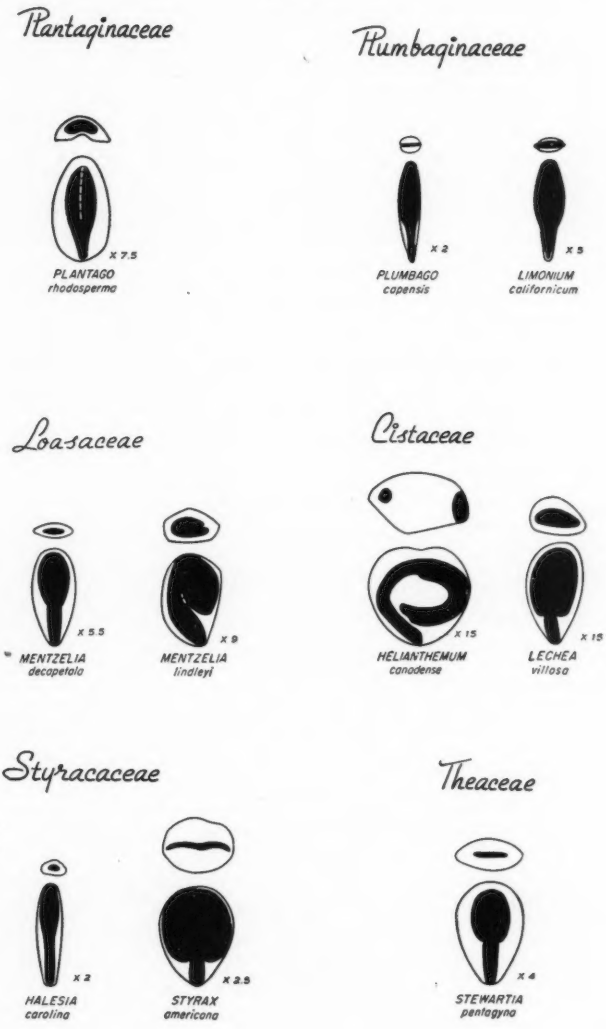
Styracaceae—Endosperm is soft to firm-fleshy.

Halesia (2 sp.) *carolina* L.; row III, 1.

Styrax (6 sp.) *americana* Lam.; row III, 2.

Theaceae—For the listing of Stewartia and other genera of this family refer to the Investing type, page 644.

PLATE 46


Plantaginaceae
x 7.5
PLANTAGO
rhodosperma
Plumbaginaceae
x 2
PLUMBAGO
capensis
x 5
LIMONIUM
californicum
Loasaceae
x 5.5
MENTZELIA
decapetala
x 9
MENTZELIA
lindleyi
Cistaceae
x 15
HELIANTHEMUM
canadense
x 15
LECHEA
villosa
Styracaceae
x 2
HALESIA
carolina
x 2.5
STYRAX
americana
Theaceae
x 4
STEWARTIA
pentagyna

SPATULATE PLATE 47

Families listed on this page have endosperm varying from fleshy to firm-fleshy except for the Turneraceae and Oxalidaceae in which it is soft-fleshy.

Apocynaceae—

Amsonia (2 sp.) *tabernaemontana* Walt.; row I, 1.
Apocynum (2 sp.) *cannabinum* L.; row I, 3.
Carissa carandas L.; row I, 5.
Nerium oleander L.; row I, 2.
Vinca rosea L.; row I, 4.

Polemoniaceae—

Collomia (2 sp.) *grandiflora Dougl.*; row III, 3.
Gilia (12 sp.); row II, 2, 3; *aggregata* (Pursh) Spreng., *gracilis* (Dougl.) Hook.—*G. aggregata* typifies the genus except for *gracilis* which is distinct and *incisa* which has a smaller embryo than the average.
Linanthus ciliatus (Benth.) Greene; row III, 2. Venation in the cotyledons is evident.
Navarretia (2 sp.) *squarrosa* (Esch.) Hook. & Arn.; row II, 1. (DWARF).
Phlox (5 sp.) *pilosa* L.; row III, 1.
Polemonium (7 sp.) *foliosissimum* Gray; row II, 4.

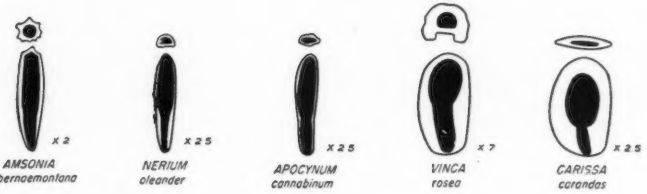
Turneraceae—*Piriqueta* sp.; row IV, 1.

Trochodendraceae—*Cercidiphyllum japonicum* Sieb. & Zucc.; row IV, 2.

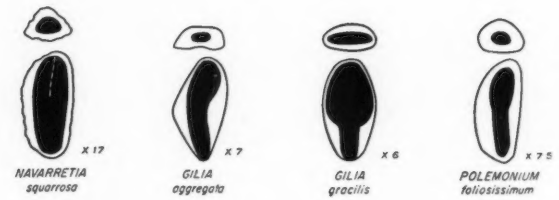
Oxalidaceae—*Oxalis* (3 sp.) *stricta* L.; row IV, 3.

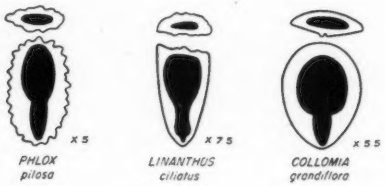
PLATE 47

Apocynaceae



Polemoniaceae





Turneraceae

Trochodendraceae

Oxalidaceae

SPATULATE PLATE 48

Oleaceae—Endosperm is firm-fleshy.

Chionanthus virginica L.; row I, 4.

Forestiera (3 sp.) *angustifolia* Torr.; row II, 2.

Fraxinus (10 sp.; 4 other species in collection sterile); row I, 1, 2, 3; *excelsior* L., *oregona* Nutt., *quadrangulata* L. (RUDIMENTARY).—*F. quadrangulata* and *excelsior* are unique as judged from material in the seed collection; other species resemble *oregona*. The genus is unusual in having representation of both Rudimentary and Spatulate types.

Ligustrum (8 sp.) row III, 1, 2; *lucidum* Ait., *vulgare* L. — *L. amurense* and *nepalense* resemble *lucidum;* other species are similar to *vulgare*.

Olea europa L.; row II, 3.

Osmanthus americanus (L.) Benth. & Hook.; row II, 4.

Syringa (5 sp.) *vulgaris* L.; row II, 1.

**Mendora* (3 sp.) (practically no endosperm).

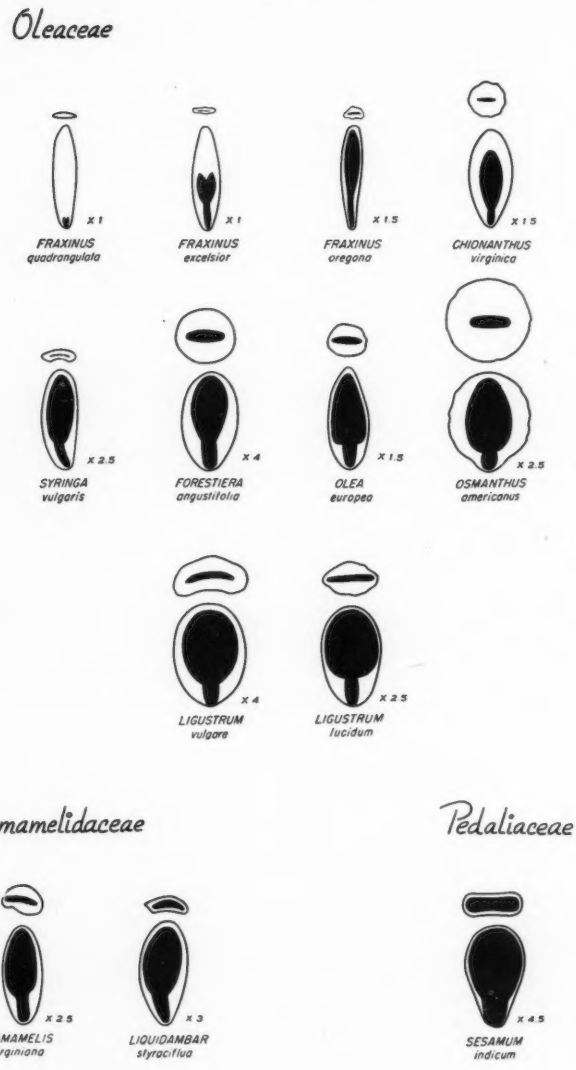
Hamamelidaceae—Endosperm is fleshy.

Hamamelis (2 sp.) *virginiana* L.; row IV, 1.

Liquidambar styraciflua L.; row IV, 2.

Pedaliaceae—Endosperm is fleshy. *Sesamum indicum* L.; row IV, 3.

PLATE 48


Oleaceae
x1
FRAXINUS quadrangulata
x1
FRAXINUS excelsior
x1.5
FRAXINUS oregona
x1.5
CHIONANTHUS virginica
x2.5
SYRINGA vulgaris
x4
FORESTIERA angustifolia
x1.5
OLEA europea
x2.5
OSMANTHUS americanus
x4
LIGUSTRUM vulgare
x2.5
LIGUSTRUM lucidum
Hamamelidaceae
x2.5
HAMAMELIS virginiana
x3
LIQUIDAMBAR styraciflua
Pedaliaceae
x4.5
SESAMUM indicum

SPATULATE PLATE 49

Cornaceae—

Cornus (21 sp.) row I, 1, 2, 3; *amomum* Mill., *canadense* L., *florida* L.—*C. nuttallii, sessilis* and *mas resemble florida; canadensis* is unique; all other species resemble *amomum*. The endosperm is soft-fleshy.

Nyssa (3 p.) *biflora* Walt.; row I, 4. Endosperm is fleshy.

Bixaceae—Endosperm is firm-fleshy. *Amoreuxia palmatifida* Moc. & Sesse; row II, 1.

Passifloraceae—*Passiflora* (5 sp.); row II, 2, 3; *incarnata* L., *pallida* L.—*P. filipes* and *lutea* are intermediate between the two species illustrated; *P. ligularis* resembles *incarnata*. The endosperm is soft-fleshy.

Violaceae—Endosperm is soft-fleshy.

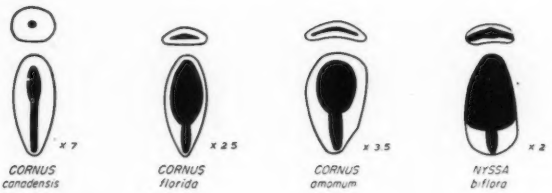
Hybanthus (2 sp.) *concolor* (Forst.) Spreng.; row III, 2.

Viola (19 sp.) *eriocarpa* Schwein.; row III, 1.

Caricaceae—Endosperm is soft-fleshy. *Carica papaya* L.; row III, 3.

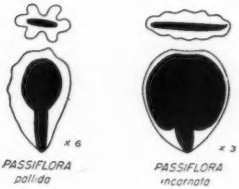
PLATE 49

Cornaceae

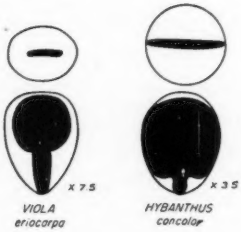


Bixaceae

Passifloraceae



Violaceae



Caricaceae

SPATULATE PLATE 50

Boraginaceae—The family is listed in floras as lacking endosperm and is largely so; there are 4 genera with evident endosperm, 18 without. A few genera are partly investing. The endosperm, when present, is fleshy to soft-fleshy.

Coldenia (2 sp.) *canescens* DC.; row I, 4. Besides the evident endosperm on the lower half of the seed there is a thin covering of it elsewhere.

Ehretia anacua (Berl.) Johnston; row I, 1. (LINEAR).

Heliotropium (12 sp.) *curassavicum* L.; row I, 2. In some species the embryo is curved.

Tournefortia gnaphalodes (Jacq.) R. Br.; row I, 3.

**Allocarya* (2 sp.)
**Amsinckia* (7 sp.)
**Anchusa* (2 sp.)
**Asperugo*
**Borago*
**Bourreria* (2 sp.)
**Cryptantha* (11 sp.)
**Cynoglossum* (2 sp.)
**Echidocarya*
**Echium*
**Eritrichium*
**Lappula* (6 sp.)
**Lithospermum* (7 sp.)
**Mertensia* (2 sp.)
**Myosotis* (3 sp.)
**Onosmodium* (3 sp.)
**Oreocarya* (2 sp.)
**Plagiobothrys* (4 sp.)

Verbenaceae—Endosperm, when present is fleshy or soft-fleshy.

Callicarpa (3 sp.) *americana* L.; row II, 1.

Lantana (4 sp.) *involucrata* L.; row II, 4.

Lippia (3 sp.) *ligustrina* (Lag.) Britton; row II, 2. In *L. lanceolata* and *nodiflora* the endosperm lining is almost negligible.

Vitex agnus-castus L.; row II, 3. —
**Avicennia.*
**Citharexylum* (2 sp.) Endosperm present as a thin negligible lining in this and the two following genera.
**Clerodendron* (INVESTING).
**Verbena* (14 sp.)

Urticaceae—Endosperm is fleshy.

Boehmeria cylindrica (L.) Sw.; row III, 2.

Hesperocnide tenella Torr.; row III, 3.

Laportea canadensis (L.) Gaud.; row IV, 3.

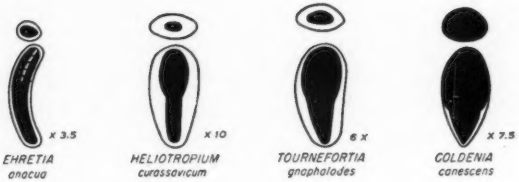
Parietaria (2 sp.) *pennsylvanica* Muhl.; row IV, 1.

Pilea pumila (L.) Gray; row III, 1.

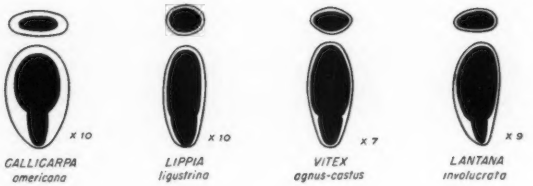
Urtica (4 sp.) *lyalli* Wats.; row IV, 2.

PLATE 50

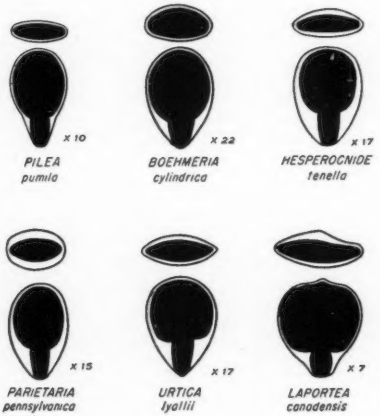
Boraginaceae



Verbenaceae



Urticaceae



SPATULATE PLATE 51

Dipsacaceae—Endosperm is fleshy.
Dipsacus (2sp.) *sylvestris* Huds.; row I, 1.
Scabiosa (3 sp.); row I, 2, 3; *caucasica* Bieb., *japonica* Miq.
S. atropurpurea resembles *japonica*.

Labiatae—This family as indicated in the statement on plate 51 belongs in the Investing type. A listing of all genera studied in the family is given on page 646. The eleven endospermous genera (of thirty-eight studied) are all Spatulate and are depicted on the opposite plate in preference to seriously interrupting continuity in illustrations for the Investing type by including them with the latter.

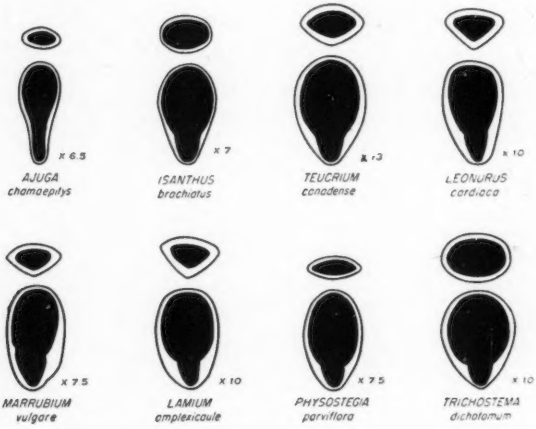
Ajuga chamaepitys Schreb.; row II, 1.
Galeopsis tetrahit L.; row IV, 3.
Isanthus brachiatus (L.) B.S.P.; row II, 2.
Lamium amplexicaule L.; row III, 2.
Leonurus cardiaca L.; row II, 4.
Marrubium vulgare L.; row III, 1.
Molucella laevis L.; row IV, 1.
Physostegia parviflora Nutt.; row III, 3.
Stachys (8 sp.) *albens* Gray; row IV, 2.
Teucrium (2 sp.) *canadense* L.; row II, 3.
Trichostema (2 sp.) *dichotomum* L.; row III, 4.

PLATE 51

Dipsacaceae

Labiatae

NOTE The Labiatae as a family is investing, though its albuminous seeds (below) are Spatulate.



SPATULATE PLATE 52

Euphorbiaceae—Endosperm is soft-fleshy to fleshy.

Acalypha (6 sp.) *virginica* L.; row IV, 1.

Adelia vaseyi (Coult.) Pax & Hoffm.; row IV, 2.

Caperonia palustris St. Hil.; row IV, 4.

Croton (17 sp.); row III, 1,2; *capitatus* Michx., *punctatus* Jacq. *C. punctatus* is typical of most species in the genus; *capitatus* is extreme in the breadth of cotyledons.

Crotonopsis linearis Michx.; row I, 4.

Ditaxis (8 sp.) *serrata* (Torr.) Heller; row I, 3. Considerable variation in the genus; in *D. aphoroides* the cotyledons are unusually large and the stalk short.

Eremocarpus setigerus (Hook.) Benth.; row III, 3.

Euphorbia (56 sp.); row II, 1, 2, 3, 4; *bicolor* Engelm., *dentata* Michx., *lathyrus* L., *vermiculata* Raf. *E. bicolor* is representative of 2 species; *dentata* of 7; *lathyrus* of 12; *vermiculata* of 35 in the Chamaesyce section.

Phyllanthus (4 sp.) *carolinensis* Walt.; row I, 2.

Reverchonia arenaria Gray; row I, 1. (LINEAR).

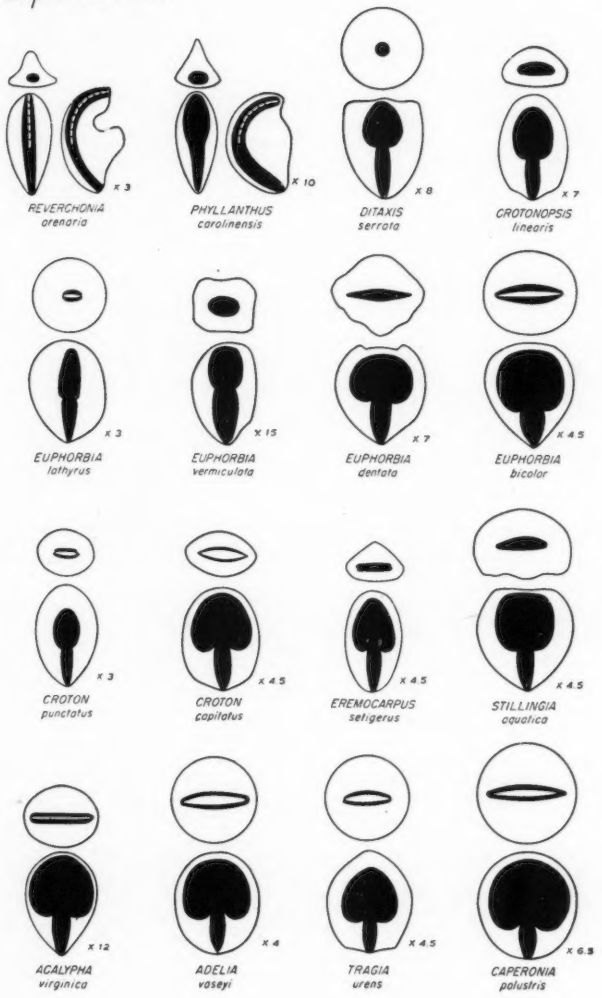
Stillingia (8 sp.) *aquatica* Chapm.; row III, 4. Genus is uniform except in *S. sylvatica* which has broader cotyledons and *paucidentata* in which the cotyledons are very narrow.

Tragia (3 sp.) *urens* L.; row IV, 3.

(Euphorbiaceae continued on plate 53)

PLATE 52

Euphorbiaceae



SPATULATE PLATE 53

Euphorbiaceae, concl.

Aleurites (3 sp.) *cordata* R. Br.; row I, 3.

Cnidoscolus (2 sp.) *texanus* (Muell. Arg) Small; row II, 3.

Jatropha (2 sp.) *spathulata* (Ort.) Muell. Arg.; row I, 4.

Manihot angustiloba (Torr.) Muell. Arg.; row II, 2.

Ricinus communis L.; row II, 1.

Sapium sebiferum (L.) Roxb.; row I, 2.

Sebastiana ligustrina (Michx.) Muell. Arg.; row I, 1.

Asclepiadaceae—Endosperm firm-fleshy.

Acerates (2 sp.) *viridiflora* (Raf.) Eaton; row III, 1.

Asclepias (12 sp.) *humistrata* Walt.; row III, 4.

Gonolobus laevis Michx.; row III, 3.

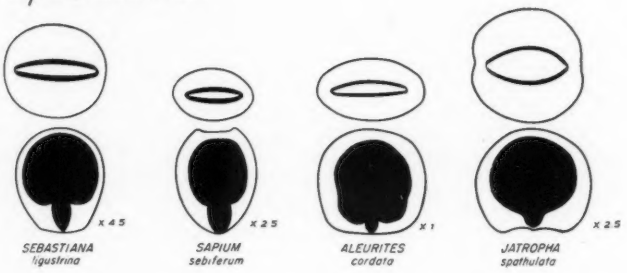
Vincetoxicum obliquum (Jacq.) Britton; row III, 2.

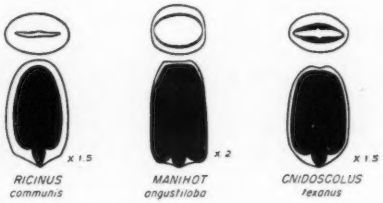
Polygalaceae—Endosperm soft-fleshy.

Polygala (11 sp.); row IV, 1, 2; *grandiflora* Walt., *sanguinea* L. *P. grandiflora* represents two species and *sanguinea* nine.

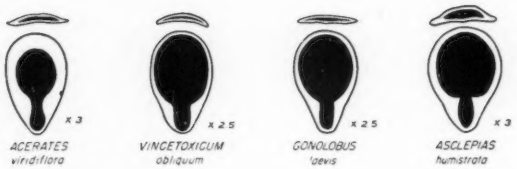
PLATE 53

Euphorbiaceae Cont

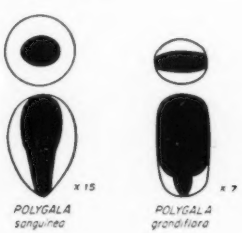




Asclepiadaceae



Polygalaceae



SPATULATE PLATE 54

Rutaceae—Endosperm is soft-fleshy or fleshy except in Porlieria in which it is hard.

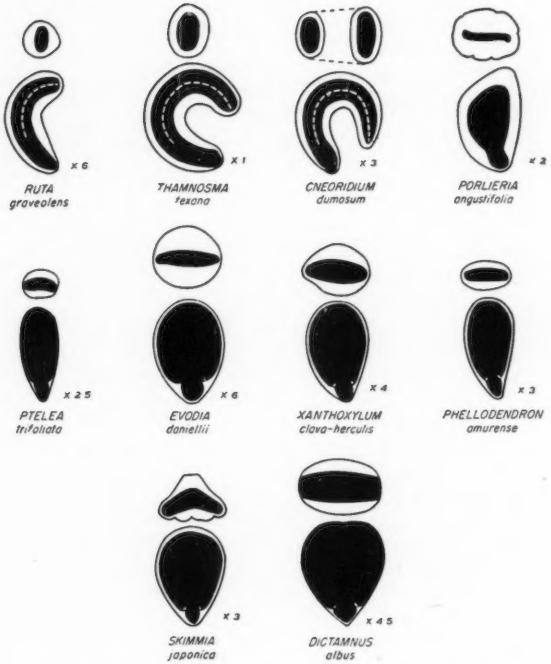
Cneoridium dumosum (Nutt.) Hook. f.; row I, 3. (LINEAR).
Dictamnus albus L.; row III, 2.
Evodia daniellii Hemsl.; row II, 2.
Phellodendron (2 sp.) *amurense* Rupr.; row II, 4.
Porlieria angustifolia (Engelm.) Gray; row I, 4.
Ptelea (2 sp.) *trifoliata* L.; row II, 1.
Ruta graveolens L.; row I, 1. (LINEAR).
Skimmia japonica Thunb.; row III, 1.
Thamnosma texana (Gray) Torr.; I, 2. (LINEAR).
Xanthoxylum (4 sp.) *clava-herculis* L.; row II, 3.
**Citrus* (6 sp.) (INVESTING).
**Fortunella* (2 sp.) (INVESTING).
**Poncirus* (INVESTING).

Fouquieriaceae—Endosperm firm-fleshy. *Fouquieria splendens* Engelm.; row IV, 1.

Flacourtiaceae—Endosperm watery-fleshy. *Xylosma flexuosa* Hemsl.; row IV, 2.

PLATE 54

Rutaceae



Fouquieriaceae

Flacourtiaceae

SPATULATE PLATE 55

Celastraceae—Endosperm fleshy or watery-fleshy.

Celastrus (2 sp.) *scandens* L.; row I, 3.

Euonymus (8 sp.) *atropurpureus* Jacq.; row I, 2. In *E. alatus* the embryo is comparatively small and in *europaeus* and *japonicus* it is large.

Maytenus (2 sp.) *phyllanthoides* Benth.; row II, 2. *M. boaria* has a smaller embryo.

Pachystima (2 sp.) *myrsinites* (Pursh) Raf.; row I, 1.

Rhacoma ilicifolia (Poir.) Trel.; row II, 1.

Schaefferia cuneifolia Gray; row I, 4.

Sapotaceae—Endosperm fleshy except in Sapota which is hard.

Bumelia (2 sp. *lanuginosa* (Michx.) Pers.; row III, 4. *B. lycioides* has even less endosperm.

Chrysophyllum oliviforme Lam.; row III, 1.

Dipholis salicifolia (L.) A. DC.; row III, 3.

Sapota achras Mill.; row III, 2.

Meliaceae—Endosperm fleshy.

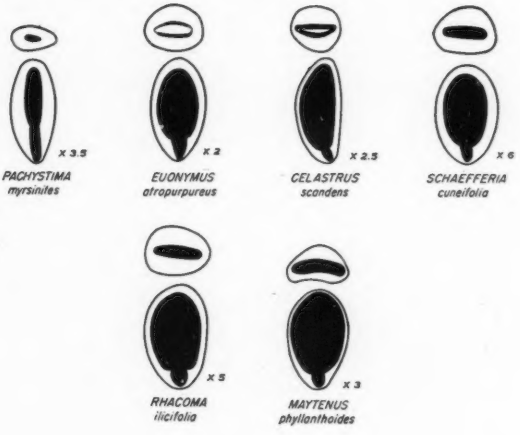
Cedrela sinensis Juss.; row IV, 2.

Melia azedarach L.; row IV, 1.

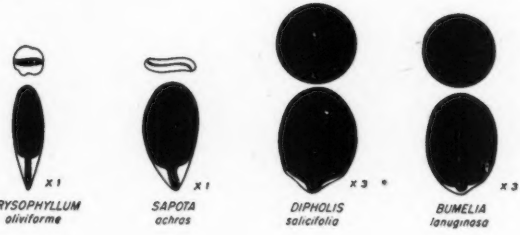
**Swietenia* (INVESTING).

PLATE 55

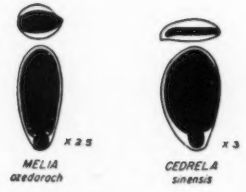
Celastraceae



Sapotaceae



Meliaceae



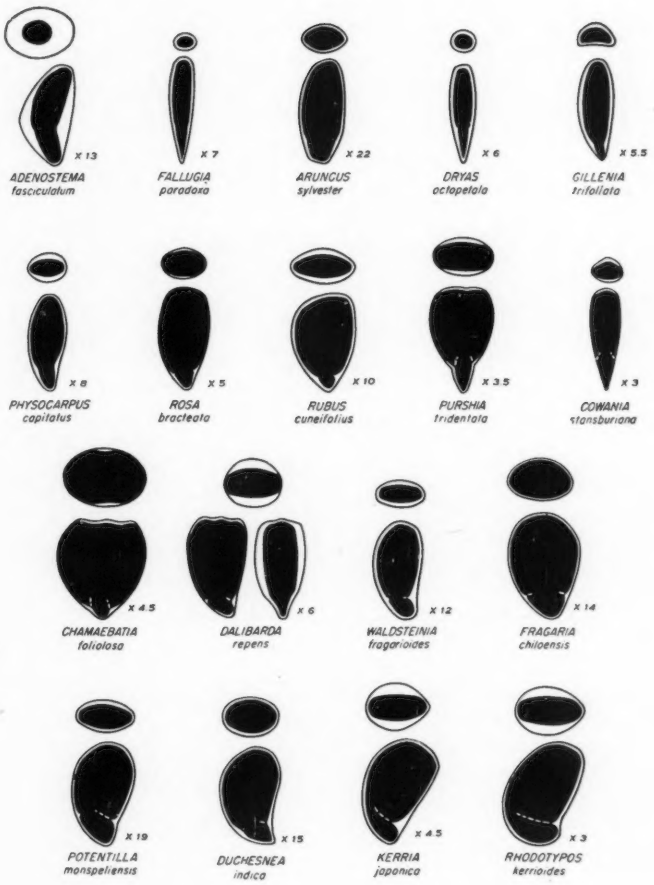
SPATULATE PLATE 56

Rosaceae—This family combines typical Spatulate genera with several in which the embryo is slightly bent or partly investing. Several genera illustrated border on "endosperm negligible." Endosperm soft-fleshy in Adenostoma; fleshy in others.

Adenostoma fasciculatum Hook. & Arn.; row I, 1.
Aruncus sylvester Kostel.; row I, 3. Endosperm lining almost negligible.
Chamaebatia foliolosa Benth.; row III, 1.
Cowania stansburiana Torr.; row II, 5.
Dalibarda repens L.; row III, 2, 3.
Dryas octopetala L.; row I, 4.
Duchesnea indica (Andr.) Focke; row IV, 2.
Fallugia paradoxa (D. Don) Endl.; row I, 2.
Fragaria (3 sp.) *chiloensis* Decne.; row III, 5. Endosperm lining barely thick enough to illustrate.
Gillenia trifoliata (L.) Moench; row I, 5.
Kerria japonica DC.; row IV, 3.
Physocarpus (7 sp.) *capitatus* (Pursh) Ktze.; row II, 1.
Potentilla (23 sp.) *monspeliensis* L.; row IV, 1. *P. anserina, palustris* and *tridentata* have the embryo nearly straight.
Purshia tridentata (Pursh) DC.; row II, 4.
Rhodotypos kerrioides Sieb. & Zucc.; row IV, 4.
Rosa (29 sp.) *bracteata* Wendl.; row II, 2. Endosperm almost negligible.
Rubus (18 sp.) *cuneifolius* Pursh; row II, 3.
Waldsteinia fragarioides (Michx.) Tratt.; row III, 4.
**Agrimonia* (6 sp.) (INVESTING).
**Cercocarpus* (3 sp.)
**Exochorda* (INVESTING).
**Geum* (8 sp.)
**Holodiscus*
**Sanguisorba* (4 sp.)
**Sibbaldia*
**Spiraea* (8 sp.)

PLATE 56

Rosaceae



SPATULATE PLATE 57

Malaceae—In this family (or subfamily) as in the Rosaceae some of the genera have a lining of fleshy endosperm barely thick enough to depict in proper proportion. Several genera are partly Investing.

Amelanchier (10 sp.) *canadensis* (L.) Medic.; row I, 3. (BENT).

Aronia (4 sp.) *arbutifolia* (L.) Ell.; row I, 1.

Cotoneaster (14 sp.) *divaricata* Rehd. & Wils.; row II, 3.

Crataegus (47 sp.) *mollis* (Torr. & Gray) Scheele; row I, 2. *C. uniflora* is unusual in having two seeds per carpel, one with a bent stalk and the other straight or nearly so.

Cydonia oblonga Mill.; row III, 2.

Malus (13 sp.) *atrosanguinea* Schneid.; row III, 1. Genus uniform except for *M. pumila* which has almost no endosperm.

Peraphyllum ramosissimum Nutt.; row III, 3.

Photinia (4 sp.) *arbutifolia* (Ait.) Lindl.; row II, 4.

Pyracantha (2 sp.) *coccinea* Roem.; row II, 2.

Sorbus (3 sp.) *aucuparia* L.; row II, 1.

**Chaenomeles* (INVESTING).

**Eriobotrya* (INVESTING).

**Pyrus* (4 sp.) (INVESTING).

**Raphiolepis* (2 sp.) (INVESTING).

Amygdalaceae (row IV, 1)—Though the diagram for Prunus is included among Spatulate groups, this family is treated under the Investing type on page 644 since most of its genera are Investing.

Elaeagnaceae—Genera in this family are partly Investing. The endosperm is fleshy or firm-fleshy.

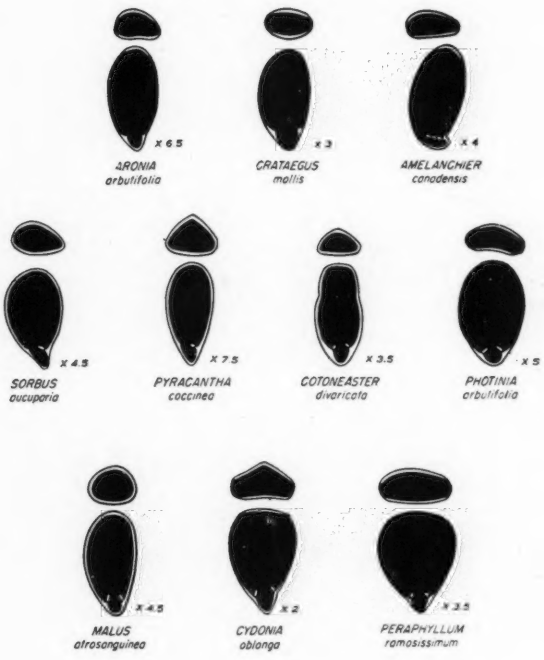
Hippophae rhamnoides L.; row IV, 2.

**Elaeagnus* (4 sp.) (INVESTING).

Shepherdia (2 sp.) *argentea* Nutt.; row IV, 3.

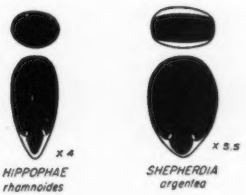
PLATE 57

Malaceae



Amygdalaceae

Elaeagnaceae



SPATULATE PLATE 58

Sterculiaceae—Endosperm fleshy to firm-fleshy. Subsequent to completion of the Sterculiaceae as represented in the Fish and Wildlife Service collection, seeds of *Brachychiton populneum* became available and were examined. They were found to represent a relatively early stage of the Spatulate type and the distinctions, both external and internal between these seeds and those of Firmiana support the recognition of the two generic names for these species in place of the inclusive one, Sterculia.

Firmiana simplex Wight; row I, 4. (INVESTING).
Fremontia californica Torr.; row I, 3.
Melochia corchorifolia L.; row I, 1.
Waltheria americana L.; row I, 2.
**Ayenia* (FOLDED).

Linaceae—*Linum* (15 sp.)*berlandieri* Hook.; row II, 1. Some variation in the genus; *L. berlandieri* is nearly average; *perenne* has much endosperm and *lewisii* very little; *usitatissimum* has almost no endosperm on edges of embryo. The endosperm is soft-fleshy.

Staphyleaceae—Endosperm is fleshy. *Staphylea* (2 sp.) *trifolia* L.; row II, 2.

Thymelaeaceae—Endosperm is fleshy. *Dirca palustris* L.; row II, 3. **Daphne* (INVESTING).

Simaroubaceae—Endosperm is fleshy.

Ailanthus altissima Swingle; row III, 2.
Castela nicholsonii Hook.; row III, 3.
Holocantha emoryi Gray; row III, 1.

PLATE 58

Sterculiaceae
x 7.5
MELOCHIA corchifolia
x 9
WALTHERIA americana
x 3.5
FREMONTIA californica
x 2.5
FIRMIANA simplex
Linaceae
x 5
LINUM berlandieri
Staphyleaceae
x 3
STAPHYLEA trifolia
Thymelaeaceae
x 3.5
DIRCA palustris
Simaroubaceae
x 3
HOLOCANTHA emoryi
x 3
AILANTHUS altissima
x 2.5
CASTELA nicholsonii

SPATULATE

*Balsaminaceae—**Impatiens* (2 sp.). Stalk very short.

*Compositae—No appreciable amount of endosperm was found in any of the 156 genera studied in this family. The stalk inclines to be proportionately large; in 26 genera it exceeds or approximately equals the length of the cotyledons while in 81 others it ranges from more than one quarter to nearly one half the length of the whole embryo. In addition the stalk of Compositae achenes has distinctive structural characteristics: commonly there is an unusually distinct core of conductive tissue occupying about one quarter of the width of the stalk or more. Also there is a rather unique, straight-line demarcation of the cotyledons from the stalk in vertical section cutting through, not between, the cotyledons. Possibly these peculiarities in the stalk of the Compositae represents a form of specialization that deserves a higher relative position than has been accorded the family.

Though cotyledons are generally well developed, they are in no case inclined toward invagination of the stalk. In the following 13 genera the cotyledons are relatively short, only about one fourth of the total embryo length: Boebera, Clappia, Ericameria, Eriophyllum, Eupatorium, Florestina, Hulsea, Palafoxia, Pectis, Pluchea, Polypteris, Trichocoronis and Tussilago. The cotyledons are broad in Actinomeris, Berlandiera, Carthamus, Melanthera, Lindheimera, Onopordon, Polymnia and Soliva as well as in Ambrosia and others of the ragweed tribe.

*Acanthospermum
*Achillea (2 sp.)
*Actinomeris
*Adenocaulon
*Agoseris (5 sp.)
*Amblyolepis
*Ambrosia (6 sp.)
*Anaphalis (2 sp.)
*Antennaria (3 sp.)
*Anthemis (3 sp.)
*Aphanostephus (3 sp.)
*Arctium (2 sp.)
*Arctotis
*Arnica (5 sp.)
*Artemisia (11 sp.)
*Aster (34 sp.)

*Baccharis (5 sp.)
*Balsamorrhiza
*Bebbia
*Bellis (2 sp.)
*Berlandiera
*Bidens (13 sp.)
*Blepharipappus
*Boebera
*Boltonia (2 sp.)
*Borrichia (2 sp.)
*Brickellia (5 sp.)

*Cacalia (2 sp.
*Callistephus
*Carduus
*Carphephorus
*Carthamus
*Centaurea (8 sp.)
*Centromadia

*Chaenactis (3 sp.)
*Chaenolobus
*Chrysanthemum (4 sp.)
*Chrysopsis
*Chrysothamnus (8 sp.)
*Cichorium (2 sp.)
*Cirsium (14 sp.)
*Clappia
*Cnicus
*Coreopsis (11 sp.)
*Corethrogyne
*Crassina
*Crepis (2 sp.)

*Dichaetophora
*Dicoria

*Echinacea (2 sp.)
*Echinops (2 sp.)
*Eclipta
*Elephantopus (2 sp.)
*Encelia (5 sp.)
*Engelmannia
*Erechtites
*Ericameria (4 sp.)
*Erigeron (13 sp.)
*Eriophyllum (4 sp.)
*Eupatorium (18 sp.)

*Flaveria (2 sp.)
*Florestina
*Franseria (5 sp.)

*Gaillardia (5 sp.)
*Galinsoga
*Gnaphalium (5 sp)
*Grindelia (4 sp.)
*Guizotia
*Gutierrezia
*Gymnolomia

*Hazardia
*Helenium (4 sp.)
*Helianthus (20 sp.)
*Heliopsis (2 sp.)
*Hemizonella
*Hemizonia (4 sp.)
*Heterotheca
*Hieracium (11 sp.)
*Hulsea
*Hymenoclea
*Hymenopappus (3 sp.)
*Hymenoxys (3 sp.)
*Hypochaeris (3 sp.)

*Inula
*Isocoma
*Iva

*Krigia (2 sp.)
*Kuhnia (3 sp.)

*Lactuca (6 sp.)
*Lagophylla
*Layia (3 sp.)
*Leontodon
*Liatris (10 sp.)
*Lindheimera

*Machaeranthera (4 sp.)
*Madia (3 sp.)
*Matricaria (2 sp.)

*Mauchia
*Melampodium
*Melanthera
*Microseris (3 sp.)
*Mikania

*Nabalus (7 sp.)

*Onopordon
*Oxytenia

*Palafoxia
*Parthenium (5 sp.)
*Pectis
*Pentzia
*Perezia (2 sp.)
*Pericome
*Petasites
*Picris (2 sp.)
*Pluchea (4 sp.)
*Polymnia (2 sp.)
*Polypteris (2 sp.)
*Prionopsis

*Pyrrhopappus (2 sp.)

*Ratabida (3 sp.)
*Rigiopappus
*Rudbeckia (6 sp.)

*Saussurea (2 sp.)
*Senecio (19 sp.)
*Seriocarpus (3 sp.)
*Serinia
*Sideranthus (3 sp.)
*Silphium (5 sp.)
*Silybum
*Solidago (22 sp.)
*Soliva
*Sonchus (3 sp.)
*Spilanthes
*Stephanomeria (3 sp.)
*Stokesia

*Tagetes
*Tanacetum (2 sp.)
*Taraxacum (2 sp.)

*Tetradymia (3 sp.)
*Tetraneuris
*Thelesperma (2 sp.)
*Thymophylla (2 sp.)
*Thyrsanthema
*Townsendia (3 sp.)
*Tragopogon
*Trichocoronis
*Trilisia (2 sp.)
*Tussilago

*Uropappus (2 sp.)

*Verbesina (2 sp.)
*Vernonia (6 sp.)

*Wyethia

*Xanthisma
*Xanthium (9 sp.)

*Zexmenia

---

*Cucurbitaceae

*Apodanthera
*Citrullus
*Cucumis (3 sp.)
*Cucurbita (5 sp.)
*Echinocystis (3 sp.) (INVESTING)
E. lobata is Spatulate.
*Ibervillea (2 sp.)
*Luffa
*Melothria
*Sicyos (INVESTING)

*Malpighiaceae

*Malpighia. Stalk partly invested.

*Myriaceae

*Myrmica. Stalk partly invested.

*Onagraceae

*Boisduvalia (2 sp.)
*Circaea (2 sp.)
*Clarkia (2 sp.)
*Epilobium (12 sp.)
*Gaura (5 sp.)
*Gayophytum
*Godetia (3 sp.)
*Jussiaea (8 sp.)
*Ludwigia (9 sp.)
*Oenothera (16 sp.)
*Zauschneria

*Salicaceae

*Populus (2 sp.)
*Salix (19 sp.)

*Valerianaceae

*Plectritis
*Valeriana (3 sp.)
*Valerianella

SUPPLEMENT; SPATULATE GENERA IN NON-SPATULATE FAMILIES

Acanthaceae (BENT)—*Tubiflora.*
Amygdalaceae (INVESTING)—*Prunus* (in part).
Araliaceae (RUDIMENTARY)—*Hedera.*
Berberidaceae (LINEAR)—*Berberis.*
Betulaceae (INVESTING)—*Alnus, Betula.*
Caesalpiniaceae (INVESTING) — *Bauhinia, Ceratonia, Cercis.*
Campanulaceae (DWARF)—*Platycodon.*
Caprifoliaceae (LINEAR)—*Lonicera, Sambucus.*
Ericaceae (DWARF) — *Arbutus, Arctostaphylos* (in part).
Gentianaceae (DWARF)—*Frasera.*
Labiate (INVESTING) — *Ajuga, Galeopsis, Isanthus, Lamium, Leonurus, Marrubium, Molucella, Physostegia, Stachys, Teucrium, Trichostema.*
Loganiaceae (DWARF)—*Gelsemium.*
Lythraceae (INVESTING) — **Didiplis, *Lythrum.*
Menispermaceae (LINEAR) — *Calycocarpum.*
Saxifragaceae (DWARF)—*Fendlera.*
Scrophulariaceae (DWARF)—*Chelone, Collinsia, Cordylanthus.*
Scrophulariaceae (DWARF) — *Euphrasia, Macranthera, Penstemon, Rhinanthus.*
Umbelliferae (LINEAR)—*Bowlesia, Coriandrum, Foeniculum, Petroselinum, Pimpinella.*
*Sapindaceae (FOLDED)—**Litchi.*

PLATE 59

BENT

Endosperm is fleshy in all families included on plate 59.

Moraceae—

Broussonetia papyrifera (L.) Vent.; row I, 3.
Cudrania tricuspidata Bureau; row I, 5.
Ficus (3 sp.) *carica* L.; row I, 1.
Maclura pomifera (Raf.) Schneid.; row I, 4. Botanical manuals mistakenly describe this as without endosperm.
Morus (4 sp.) *alba* L.; row I, 2.

Cannabinaceae—

Cannabis sativa L.; row II, 2.
Humulus (2 sp.) *lupulus* L.; row II, 1.

Bombacaceae—*Ceiba pentandra* Gaertn.; row II, 3.

Acanthaceae—The one endospermous and illustrated genus, Tubiflora, is only slightly bent and could have been placed among the Spatulate illustrations; in other genera, however, the embryo is strongly bent. The cotyledons of most genera are especially leaf-like in having prominent venation. Several genera are Investing.

Tubiflora carolinensis (Walt.) J. F. Gmel.; row II, 4. (SPATULATE).

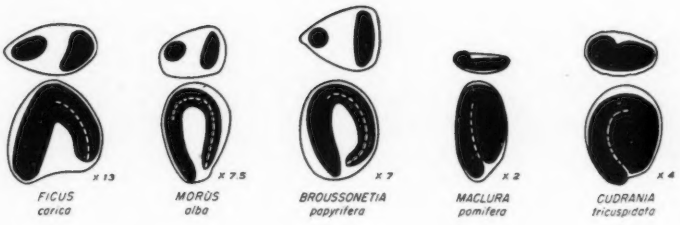
**Anisacanthus*
**Beloperone*
**Carlowrightia* (2 sp.)
**Dianthera* (3 sp.)
**Dicliptera* (2 sp.)
**Dyschoriste* (3 sp.) (INVESTING)
**Hygrophila* (INVESTING)
**Ruellia* (2 sp.) (INVESTING)
**Stenandrium* (INVESTING)
**Tetramerium*
**Thunbergia*
**Yeatesia*

Anacardiaceae—This family has been incorrectly described in some floras as lacking endosperm.

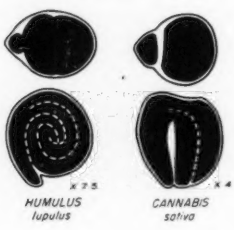
Malosma laurina (Nutt.) Nutt.; row III, 1.
Pistacia (2 sp.) *chinensis* Bunge; row III, 5.
Rhus (10 sp.) *glabra* L.; row III, 4. *R. trilobata* differs from others in having more endosperm.
Schinus (2 sp.) *molle* L.; row III, 2.
Toxicodendron (4 sp.) *diversiloba* (Torr. & Gray) Greene; row III, 3. *T. vernix* has less endosperm than others.

PLATE 59

Moraceae



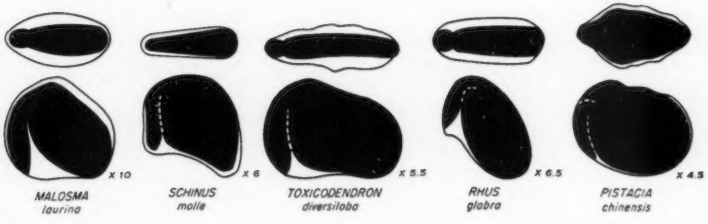
Cannabinaceae



Bombacaceae

Acanthaceae

Anacardiaceae



BENT

Fabaceae—This family (or subfamily) is distinct from the Mimosaceae, Krameriaceae and Caesalpinaceae in seed type and therefore, for present purposes, is segregated from the other groups with which it is commonly combined under the name Leguminosae.

In 75 genera studied 41 have endosperm in appreciable quantity and are illustrated. The endosperm when present is generally most abundant on the exterior face of the cotyledons but often is present in small amounts near the base of the stalk. Usually it is hard and somewhat glassy and does not give starch reaction with iodine and in these regards it resembles the endosperm of the related families, Mimosaceae and Caesalpiniaceae. In a few genera such as Sophora, Cladrastis and Crotalaria there is an accessory layer of material, "wall parenchyma," similar to that present in the Mimosaceae.

Three genera, Arachis, Chapmania and Stylosanthes, are erect and Investing but the remainder are Bent though in Amorpha and Pickeringia (Pl 60) the degree of bending is slight. The drawings have been arranged in a progressive series from the slightly bent or half bent (axis of cotyledons at right angles to the stalk) to forms in which the embryo is jackknifed with cotyledons and stalk nearly parallel and subequal in length and finally to similar forms having relatively short stalks.

The stalk is generally longest and largest in genera having considerable endosperm and appears cramped and reduced in many lacking endosperm. In general, however, repression and compression of the stalk induced by cotyledonary development seems to have been avoided in some degree by the bent position of the embryo. Whereas the stalk in advanced erect or straight embryoed seeds such as the Investing type inclines to be short and broad, it is usually relatively slender in Bent seeds lacking endosperm.

The plumule is often evident and well-developed in genera without endosperm.

The family is illustrated on plates 60, 61 and 62.

PLATE 60

BENT

Fabaceae—

Abrus precatorius L.; row IV, 3. The endosperm lining is very slight and possibly does not justify the inclusion of this genus with the endospermous group.

Aeschynomene (2 sp.) *virginica* (L.) B.S.P.; row II, 2.

Amorpha (6 sp.) *canescens* Pursh; row I, 1.

Baptisia (9 sp.) *tinctoria* (L.) R. Br.; row III, 4.

Cladrastis lutea (Michx. f.) Koch; row I, 3.

Dalea (4 sp.) *frutescens* Gray; row II, 1.

Daubentonia drummondii Rydb..; row I, 4.

Indigofera (5 sp.) *caroliniana* Walt.; row IV, 1.

Laburnum (2 sp.) *anagyroides*, Medic.; row IV, 2.

Petalostemum (4 sp.); row III, 1, 2, 3; *corymbosum* Michx., *purpureum* (Vent.) Rydb., *villosum* Nutt.—*P. villosum* is distinct as indicated in its diagram; *candidum* has practically no endosperm; *corymbosum*, sometimes classed under the genus Kuhnistera, is similar to *purpureum*.

Pickeringia montana Nutt.; row I, 2.

Robinia (2 sp.) *pseudoacacia* L.; row II, 3.

Zornia bracteata (Walt.) Gmel.; row II, 4.

PLATE 60

Fabaceae

PLATE 61

BENT

Fabaceae—(cont'd.)

Anthyllis vulneraria L.; row IV, 2.
Alhagi camelorum Fisch.; row IV, 3.
Cologania lemmoni Gray; row II, 4.
Colutea arborescens L.; row I, 3.
Cytisus (4 sp.) *scoparius* (L.) Link; row II, 1.
Genista tinctoria L.; row II, 2.
Hedysarum coronarium L.; row I, 4.
Medicago (5 sp.) *lupulina* L.; row IV, 4.
Melilotus (4 sp.) *alba* Desv.; row III, 4. *M. indica* and *gracilis* show a larger proportion of endosperm.
Oxytropis (3 sp.) *lamberti* Pursh; row II, 3.
Spartium junceum L.; row I, 2.
Trifolium (18 sp.); row III, 1, 2, 3; *dubium* Sibth., *obtusiflorum* Hook., *repens* L. — The species illustrated represent variations in endosperm as well as in proportionate length of cotyledons.
Trigonella (2 sp.) *caerulea* Ser.; row IV, 1.
Ulex europaeus L.; row I, 1.

PLATE 61

Fabaceae Cont.

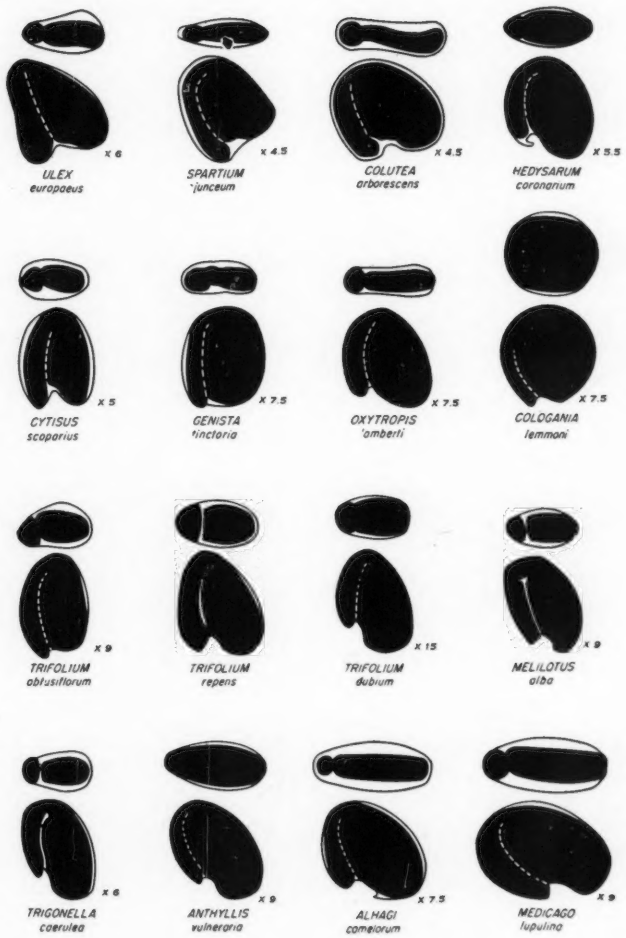


PLATE 62

BENT

Fabaceae—(concl.)

Astragalus (20 sp.) *brazoensis* Buckl.; row II, 4. There is considerable variation within the genus; 15 of the 20 species studied resemble *A. brazoensis;* 3 have more endosperm, some surrounding the stalk and evident on the edges of the seed as well as on its faces; 2 have almost no endosperm.

Coronilla scorpioides Koch; row IV, 1.

Crotolaria (8 sp.) *spectabilis* Roth; row I, 2.

Desmodium (11 sp.) *tortuosum* (Sw.) DC.; row II, 2. *D. tortuosum* is the only species of the eleven studied that has any appreciable amount of endosperm; six show only a very thin, barely visible lining and in the other four no lining is evident.

Galega officinalis L.; row I, 3.

Glottidium vesicarium (Jacq.) Harper; row IV, 2.

Glycyrrhiza (2 sp.) *lepidota* (Nutt.) Pursh; row II, 3.

Lespedeza (15 sp.) *repens* (L.) Bart.; row II, 1. *L. repens* is average for the genus in that there are five other species that resemble it, five that have a larger proportion of endosperm and four that have none or practically none.

Lotus (16 sp.) *crassifolius* (Benth.) Greene; row I, 1. There is considerable variation in the genus not only in shape and size of seeds but also in relative length of cotyledons and proportion of endosperm. *L. crassifolius* is representative of thirteen species but *grandiflorus* has endosperm evident as a layer over all parts of the embryo exterior and, at the other extreme, *formossissimus* and *corniculatus* have very little endosperm.

Ornithopus (2 sp.) *sativus* Brot.; row I, 4.

Pueraria thunbergiana (Sieb. & Zucc.) Benth.; row III, 4.

Sesbania (2 sp.) *macrocarpa* Muhl.; row III, 3.

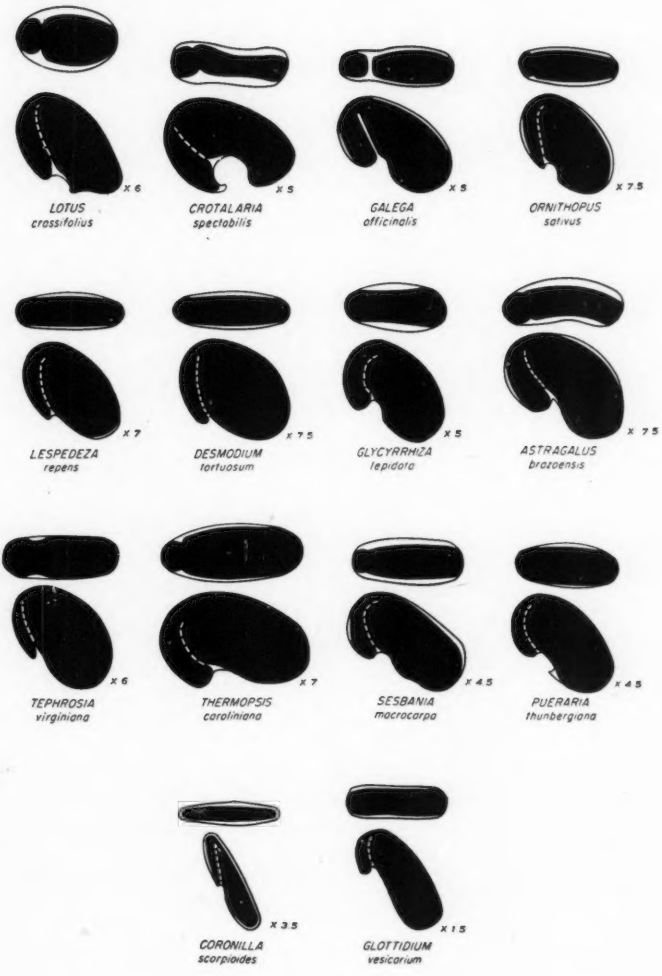
Tephrosia (6 sp.) *virginiana* (L.) Pers.; row III, 1. In four species endosperm is absent or hardly evident, in *T. virginiana* it is scant and localized and in serica there is an appreciable layer on each face.

Thermopsis (4 sp.) *caroliniana* M. A. Curtis; row III, 2.

**Amphicarpa*
**Apios*
**Arachis* (INVESTING)
**Cajanus*
**Canavalia* (2 sp.)
**Caragna*
**Centrosema*
**Chapmania* (INVESTING)
**Cicer*
**Clitoria* (2 sp.)
**Dalbergia* (2 sp.)
**Dioclea*
**Dolichos* (2 sp.)
**Erythrina*
**Galactia* (8 sp.)
**Glycine* (8 sp.)
**Lathyrus* (11 sp.)
**Lens*
**Lupinus* (32 sp.)
**Mucuna* (2 sp.)
**Olneya*
**Onobrychis*
**Phaseolus* (14 sp.)
**Pisum* (2 sp.)
**Pitcheria*
**Psoralea* (8 sp.)
**Rynchosia* (4 sp.)
**Sophora* (3 sp.)
**Strophostyles* (3 sp.)
**Stylosanthes* (3 sp.) (INVESTING)
**Vicia* (21 sp.)
**Vigna* (2 sp.) This and Strophostyles are the only two legume genera in which a cavity was noted between the cotyledons.
**Voandzeia*
**Wisteria* (4 sp.) In some instances the stalk appears partially invested.

PLATE 62

Fabaceae Concl.



BENT

*Cruciferae—The thirty-two genera studied in this family are all without endosperm. All are Bent but the cotyledons are disposed in at least four different positions: incumbent, oblique (intermediate between incumbent and accumbent), accumbent and conduplicate. The order in which these four groups are listed represents a more or less progressive series in extent of cotyledonary development.

INCUMBENT

Camelina (2 sp.)
Capsella
Conringia
Coronopus
Descuhainia (5 sp.)
Erysimum (3 sp.)
Hesperis
Isatis
Lepidium (10 sp.)—*L. virginicum* is accumbent.
Stanleya (2 sp.)

OBLIQUE

Sisymbrium (4 sp.)
Eutrema

ACCUMBENT

Arabis (6 sp.)
Athysanus
Berteroa
Barbarea (3 sp.)
Cakile
Cardamine
Dentaria
Dithyrea
Draba (4 sp.)
Lesquerella
Lobularia
Matthiola
Nasturtium
Parrya
Radicula (4 sp.)
Synthlipsis
Thelypodium
Thysanocarpus — The accumbent genera Barbarea, Berteroa and Nasturtium are somewhat oblique.

CONDUPLICATE (FOLDED slightly)

Brassica (9 sp.)
Raphanus (2 sp.)

SUPPLEMENT; BENT GENERA IN NON-BENT FAMILIES

Cistaceae (SPATULATE)—*Helianthemum.*
Labiatae (INVESTING)—**Scutellaria.*
Loasaceae (SPATULATE)—*Mentzelia*
Malaceae (SPATULATE)—*Amelanchier.*
Rhamnaceae (INVESTING)—**Exothea.*
Ulmaceae (INVESTING)—*Trema.*
*Aceraceae (FOLDED)—**Acer* (in part).
*Myrtaceae (FOLDED)—**Eugenia.*
*Sapindaceae (FOLDED)—**Sapindus, *Ungnadia.*

FOLDED PLATE 63

Ulmaceae—Though two diagrams for endospermous genera are included among the Folded type on plate 63, the major number of genera are Investing and the listing for the family is given under that type on page 646.

Tiliaceae—Endosperm is fleshy. *Tilia* (5 sp.) *americana* L.; row I, 3.

Convolvulaceae—Embryo leaves in several genera of the family are punctate dotted as in a number of genera of the other major Folded family, Malvaceae. External as well as internal characteristics of seeds of these two families suggest relationship. Endosperm is hard and clear or semitransparent.

Breweria (2 sp.) *pinckeringii* (M. A. Curtis) Gray; row II, 2.

Convolvulus (8 sp.) *incanus* Vahl; row III, 2.

Cuscuta (7 sp.) *pentagona* Engelm.; row II, 1. (LINEAR). Since there are no expanded cotyledons on the embryo of this genus it is not classed as Folded.

Evolvulus (5 sp.) *sericeus* Sw.; row III, 1.

Ipomoea (18 sp.) *lacunosa* L.; row III, 3.

Jacquemontia (3 sp.) *tamnifolia* (L.) Griseb.; row II, 3.

PLATE 63

Ulmaceae
Tiliaceae
x 10
x 4
x 4
TREMA floridana
CELTIS reticulata
TILIA americana

Convolvulaceae
x 15
x 3.5
x 6
CUSCUTA pentagona
BREWERIA pickeringii
JACQUEMONTIA tamnifolia
x 7
x 5
x 3.5
EVOLVULUS sericeus
CONVOLVULUS incanus
IPOMOEA lacunosa

PLATE 64

FOLDED

Malvaceae—See comment under Convolvulaceae, page 636. Endosperm is firm-fleshy throughout the family except in Abutilon in which it is hard.

Abutilon (12 sp.) *theophrasti* Medic.; row I, 4.
Althaea (2 sp.) *rosea* Cav.; row I, 2.
Anoda (3 sp.) *cristata* (L.) Schlecht.; row IV, 3.
Callirhoe (5 sp.) *involucrata* (Nutt.) Gray; row III, 2.
Hibiscus (13 sp.) *incanus* Wendl.; row IV, 2. Genus uniform except for *H. esculentus* which has no apparent endosperm.
Kosteletzkya (2 sp.) *virginica* (L.) Gray; row II, 3. In *K. althaeifolia* endosperm is even less evident.
Lavatera assurgentiflora Kell.; row I, 3.
Malachra (2 sp.) *capitata* L.; row II, 4. Endosperm not evident in *M. urens*.
Malva (6 sp.) *rotundifolia* L.; row III, 4.
Malvastrum (10 sp.) *exile* Gray; row III, 3.
Modiola caroliniana (L.) Don; row I, 1.
Napaea dioica L.; row I, 5.
Sida (15 sp.) *rhombifolia* L.; row IV, 1.
Sidalcea (13 sp.) *neomexicana* Gray; row II, 1.
Sphaeralcea (27 sp.) *angustifolia* (Cav.) G. Don; row III, 1.
Wissadula holosericea (Scheele) Garcke; row II, 2.
**Cienfuegosia*
**Gossypium* (3 sp.)
**Malvaviscus*
**Pavonia* (3 sp.)
**Urena*

*Aceraceae—**Acer* (20 sp.) In some species such as *A. spicatum* and *negundo* the embryo instead of being Folded is Bent.

*Burseraceae—**Bursera*.

*Calycanthaceae—**Calycanthus* (2 sp.), **Meratia*.

*Geraniaceae—**Erodium* (4 sp.), **Geranium* (10 sp.), **Pelargonium*.

*Myrtaceae—**Calyptranthes*, **Eucalyptus* (12 sp.), **Eugenia* (4 sp.) (BENT), **Myrtus* (LINEAR).

*Phrymaceae—**Phryma*.

*Punicaceae—**Punica*.

*Sapindaceae—**Cardiospermum*, **Dodonaea*, **Koelreuteria*, **Litchi* (SPATULATE), **Sapindus* (3 sp.) (BENT), **Ungnadia* (BENT).

SUPPLEMENT; FOLDED GENERA IN NON-FOLDED FAMILIES.

Amygdalaceae (INVESTING)—**Osmaronia*.
Caesalpiniaceae (INVESTING)—*Cassia tora*.
Sterculiaceae (SPATULATE)—**Ayenia*.
Theaceae (INVESTING)—**Gordonia*.
Ulmaceae (INVESTING)—*Celtis*.
*Cruciferae (BENT)—**Brassica*, **Raphanus*.
*Fagaceae (INVESTING)—**Fagus*.

PLATE 64

Malvaceae

PLATE 65

INVESTING

Rhamnaceae—Endosperm is fleshy.

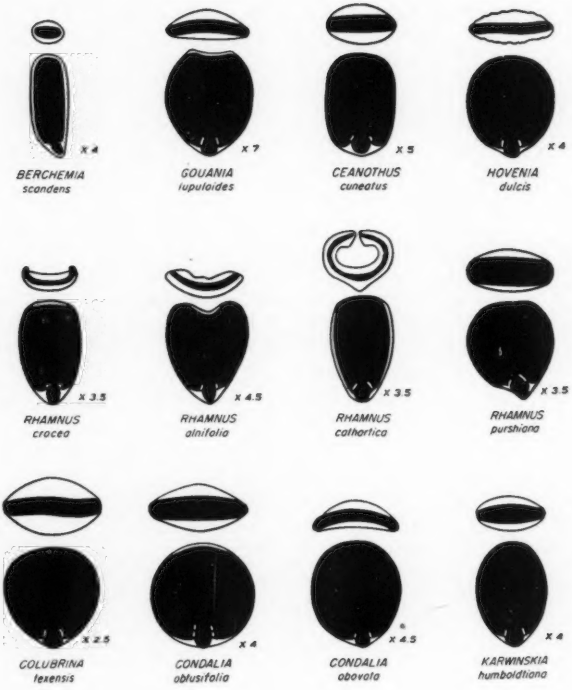
Berchemia (3 sp.) *scandens* (Hill.) Trel.; row I, 1.
Ceanothus (20 sp.) *cuneatus* (Hook.) Nutt.; row I, 3.
Colubrina (2 sp.) *texensis* (Torr. & Gray) Gray; row III, 1.
Condalia (3 sp.); row III, 2, 3; *obovata* Hook., *obtusifolia* (Hook.) *Weberb.* —*C. obtusifolia* is sometimes classed under the separate genus *Zizyphus*.
Gouania lupuloides (L.) Urban; row I, 2.
Hovenia dulcis Thunb.; row I, 4.
Karwinskia humboldtiana (Roem. & Schult.) Zucc.; row III, 4.
Rhamnus (12 sp.); row II, 1, 2, 3, 4; *alnifolia* L'Her., *cathartica* L., *crocea* Nutt., *purshiana* DC.
**Exothea* (BENT), **Reynosia*.

Betulaceae—Endosperm is fleshy.

Alnus (8 sp.) *rugosa* (Ehrh.) Spreng. (SPATULATE); row IV, 1.
Betula (9 sp.) *lenta* L. (SPATULATE); row IV, 2.
Carpinus (4 sp.) *caroliniana* Walt.; row IV, 3.
Ostrya (2 sp.) *virginiana* K. Koch; row IV, 4.
**Corylus* (4 sp.)

PLATE 65

Rhamnaceae



Betulaceae

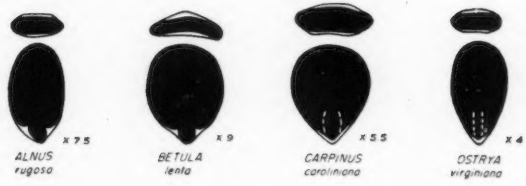


PLATE 66

INVESTING

Caesalpiniaceae—Of the twelve genera studied, eleven have evident endosperm, frequently around the base of the embryo as well as opposite the cotyledon faces. A layer of wall parenchyma is also present. The endosperm is hard and glass-like.

Bauhinia purpurea L. (SPATULATE); row II, 2. Bauhinia is on the borderline between Spatulate and Investing.

Cassia (19 sp.) row I, 1, 2, 3, 4; *fasciculata* Michx., *ligustrina* L., *occidentalis* L., *tora* L. (FOLDED).

Ceratonia siliqua L. (SPATULATE); row II, 3.

Cercidium floridum Benth.; row II, 4.

Cercis (4 sp.) *canadensis* L. (SPATULATE); row II, 1.

Gleditsia (3 sp.) *triacanthos* L.; row III, 1.

Gymnocladus dioica (L.) Koch; row IV, 2.

Hoffmanseggia (4 sp.) *densiflora* Benth.; row IV, 1.

Parkinsonia aculeata L.; row III, 3.

Poinciana (3 sp.) *gilliesii* Hook.; row III, 4.

Schrankia (2 sp.) *uncinata* Willd.; row III, 2.

**Guilandina.*

PLATE 66

Caesalpiniaceae

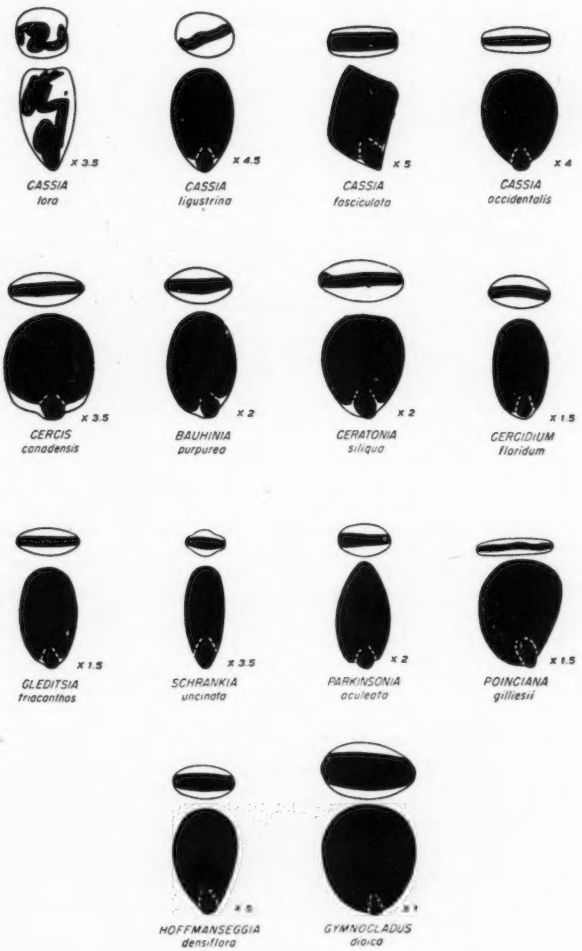


PLATE 67

INVESTING

Mimosaceae—Of the genera studied in the family six have evident endosperm. It is hard and glass-like and is present most abundantly on the cotyledon faces. As in the Caesalpiniaceae all genera have wall parenchyma, usually a dark brown layer of varying thickness. The plumule is conspicuously developed in Acacia, Adenanthera, Albizzia, and Calliandra.

Adenanthera pavonina L.; row II, 3.

Desmanthus (2 sp.) *illinoensis* (Michx.) MacM.; row I, 3. As in Albizzia there are strands of endosperm-like material in the wall parenchyma, toward the narrow edges of the seed.

Leucaena glauca (L.) Benth.; row I, 4.

Mimosa (4 sp.) *biuncifera* (Benth.) Britt. & Rose; row I, 2.

Neptunia floridana Small; row I, 1.

Prosopis (3 sp.); row II, 1, 2; *chilensis* (Mol.) Stuntz, *pubescens* Benth.

**Acacia* (13 sp.)

**Albizzia* (3 sp.) This genus may not be without endosperm; cross sections show a small island of glassy endosperm-like material at either end, surrounded by wall parenchyma. In *A. lophantha* this material is very conspicuous, in *julibrissin* it is small and in *lebbek* it is conspicuous.

**Calliandra*, **Lysiloma*, **Pithocellobium* (3 sp.)

Lythraceae—This family, despite the diagram for Rotala on the final plate for the Investing type, is not a typical representative of the group. Two of the six genera are Spatulate and further than that the family is anomalous in having at least two Investing genera that apparently incline toward the Dwarf type.

Rotala ramosior (L.) Koehne; row III.

Ammannia* (3 sp.),Cuphea*, **Decodon*, **Didiplis* (SPATULATE), **Lythrum* (SPATULATE).

Theaceae (Plate 46)—The only endospermous genus studied in this family, Stewartia, is illustrated on plate 46 with other Spatulate groups. Two genera are Investing, one Folded and one Spatulate.

Stewartia (2 sp.) *pentagyna* L'Her. (SPATULATE).

**Camellia* (3 sp.), **Gordonia* (FOLDED), **Thea*.

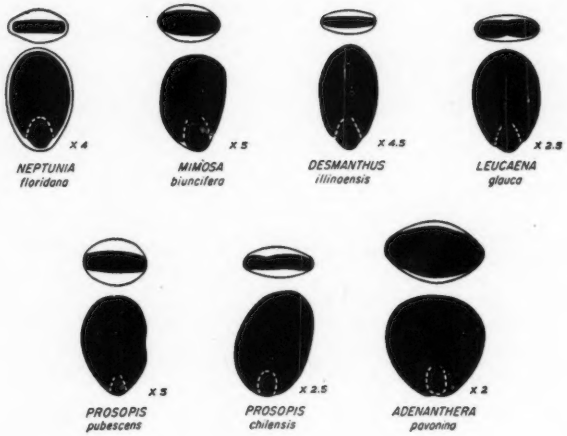
Amygdalaceae (Plate 57)—Three different types are represented in the three genera studied: Investing in Chrysobalanus and in part of Prunus, Spatulate in part of Prunus and Folded in Osmaronia.

Prunus (27 sp.) *angustifolia* Marsh. Twenty species studied are like *P. angustifolia* in being endospermous and Spatulate or only partly Investing; six species (*P. armeniaca, carolina, commune, ilicifolia, lyoni* and *persica*) have no endosperm or practically none and are Investing and one species (*myrtifolia*) is without endosperm and Spatulate.

**Chrysobalanus* (2 sp.), **Osmaronia* (FOLDED).

PLATE 67

Mimosaceae



Lythraceae

Labiatae (Plate 51)—The eleven endospermous genera studied in this family are all Spatulate and are included among illustrations for that type on plate 51. With one exception, Scutellaria (Bent), the remaining genera are Investing. The endosperm is fleshy except in Stachys and Teucrium in which it is soft-fleshy.

Ajuga chamaepitys Schreb. (SPATULATE).
Galeopsis tetrahit L. (SPATULATE).
Isanthus brachiatus (L.) B.S.P. (SPATULATE).
Lamium amplexicaule L. (SPATULATE).
Leonurus cardiaca L. (SPATULATE).
Marrubium vulgare L. (SPATULATE).
Molucella laevis L. (SPATULATE).
Physostegia parviflora Nutt. (SPATULATE).
Stachys (8 sp.) *albens* Gray (SPATULATE).
Teucrium (2 sp.) *canadense* L. (SPATULATE).
Trichostema (2 sp.) *dichotomum* L. (SPATULATE).

**Agastache* (4 sp.)
**Audibertia*
**Clinopodium* (3 sp.)
**Collinsonia*
**Cunila*
**Dicerandra*
**Dracocephalum*
**Hedeoma* (3 sp.)
**Hyptis* (2 sp.)
**Hyssopus*
**Lavandula*
**Lycopus* (6 sp.)
**Melissa*
**Mentha* (3 sp.)
**Micromeria*
**Monarda* (5 sp.)
**Monardella* (4 sp.)
**Nepeta*
**Origanum*
**Perilla*
**Prunella*
**Pycnanthemum* (3 sp.)
**Salvia* (15 sp.)
**Satureia*
**Scutellaria* (5 sp.) (BENT)
**Sphacele*
**Thymus*

Ulmaceae (Plate 63)—The endospermous genera studied in this family are figured on plate 63. Three types are represented in the five genera.

Celtis (10 sp.) *reticulata* Torr. (FOLDED).
Trema floridana Britton (BENT).
**Planera*, **Ulmus* (6 sp), **Zelkova*.

*Bignoniaceae—**Catalpa* (2 sp.), **Chilopsis* (3 sp.), **Jacaranda*, **Spathodea*, **Tacoma* (2 sp.).
*Fagaceae—**Castanea* (4 sp.), **Castanopsis*, **Fagus* (2 sp.), (FOLDED), **Lithocarpus*, **Quercus* (35 sp.).
*Juglandaceae—**Carya* (8 sp.), **Juglans* (8 sp.).
*Krameriaceae—**Krameria*.
*Lauraceae—**Cinnamomum*, **Laurus*, **Lindera*, **Litsea*, **Ocotea*, **Persea* (4 sp.), **Sassafras*, **Umbellularia*.
*Limnanthaceae—**Floerkea*.
*Martyniaceae—**Martynia*.
*Proteaceae—*Grevillea*.
Tropaeolaceae—**Tropaeolum*.

SUPPLEMENT; INVESTING GENERA IN NON-INVESTING FAMILIES

Acanthaceae (BENT)—**Dyschoriste*, **Hygrophila*, **Ruellia*, **Stenandrium*.
Buxaceae (LINEAR)—**Simmondsia*.
Elaeagnaceae (SPATULATE)—**Elaeagnus*.
Fabaceae (BENT)—**Arachis*, **Chapmania*, **Stylosanthes*.
Malaceae (SPATULATE)—**Chaenomeles*, **Eriobotrya*, **Pyrus*, **Raphiolepis*.
Meliaceae (SPATULATE)—**Swietenia*.
Rosaceae (SPATULATE)—**Agrimonia*, **Exochorda*.
Rutaceae (SPATULATE)—**Citrus*, **Fortunella*, **Poncirus*.
Sterculiaceae (SPATULATE)—**Firmiana*.
Thymelaeaceae (SPATULATE)—**Daphne*.
Verbenceae (SPATULATE)—**Clerodendron*.
Zygophyllaceae (SPATULATE)—**Kallstroemia*.
*Cucurbitaceae (SPATULATE)—**Echinocystis* (part), *Sicyos*.

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To Genera and Families Analyzed

Genera not marked by asterisks have endosperm and are illustrated; those with asterisks have no endosperm and are not illustrated. Only the more important references are included.

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*Salsola	562
*Salvia	646
Sambucus	573
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Sanguinaria	554
*Sanguisorba	620
Sanicula	568
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*Sapindaceae	638
*Sapindus	638
Sapium	614
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Sapota	618
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*Sarcobatus	562
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*Sassafras	646
*Satureia	646
Saururaceae	556
Saururus	556
*Saussurea	627
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*Serinia	627
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*Sicyos	627
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*Sideranthus	627
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*Simmondsia	574
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*Stylosanthes	634
Styracaceae	600
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*Swietenia	618
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*Zannichellia	550
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Three Noteworthy Cacti of Southwestern Utah

J. S. Daston

In the spring of 1939 and 1940 Dr. Fred A. Barkley collected some unusual cacti in southwestern Utah in the vicinity of the Desert Experimental Range west of Milford. These cacti were locally known as *Opuntia fragilis*. Dr. Barkley called the author's attention to them and at the same time further collections were made by Drs. Selar Hutchings and Gordon Marsh of the U.S. Desert Experimental Range Staff.

Comparison with the genera of cacti as segregated by Britton and Rose, Alwin Berger, Marshall and Bock, C. Backeberg and F. M. Knuth and Prof. Borg indicated that these plants have claim to rank as a new genus. The plants have the characteristic roots of *Pterocactus*, natives of Argentina and Patagonia, but the areoles are without glochids typical of that genus. The small size and clavate shape of the branches exclude them from *Pterocactus*. They superficially resemble *Opuntia australis* Web. but that species likewise has glochids. In some respects they resemble *Maihuenia* of Chile and Argentina, (see Britton and Rose, Cactaceae, vol. 1) but differ in several important characteristics.

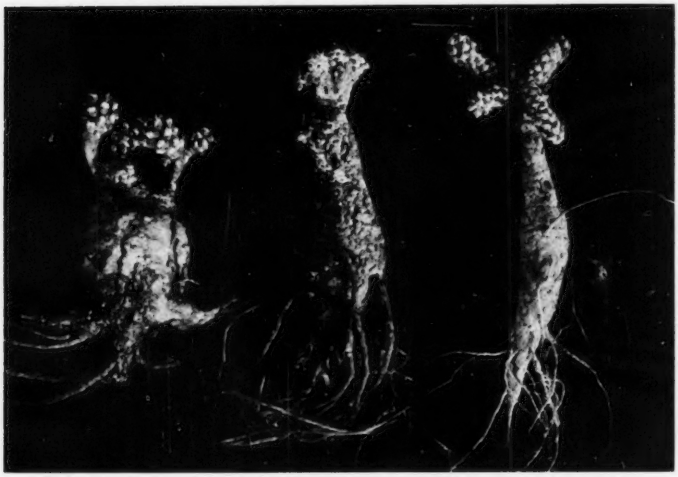
The description of this genus follows, with descriptions of the three species represented. The specimens on which the species are based were collected by Gordon Marsh in November of 1945 and in January of 1946 near the U. S. Desert Experimental Range in southwestern Utah and the type specimens are deposited in the Herbarium of the Chicago Natural History Museum. Isotypes are deposited in the Herbarium of the University of Texas, Austin, Texas.

Micropuntia gen. nov.

Plantae perennes, caulibus paucis (2 vel 3) segmentis demum crassi-claviculatis mammillatis; glochidiis nullis, aureolis depressis apice pilis capillaribus albo-villosis, foliis rudimentariis praeparvis acutis rubescentibus, spinis gracillimis flexibilibus; radialibus 5-6, centralibus solitariis (rarius 2 vel 4) basi bulbosis, leviter curvatis. Radix tuberiformis, ramis longissimis. Fructus siccus globosus aculeis intense albis armatus. Flores ignoti. — Utah: in regione limitanea, in terra fere occulta; rarissima.

Micropuntia brachyrhopalica sp. nov.

Species typica, cum characteribus generis; caulium segmentis primariis vix 3 cm. longis basim versus subviridibus alibi viridi-purpureis, spinis albidis teretibus, radialibus circa 3 mm. longis centralibus 1 incurvatis circa 0.5 cm. longis, radice obovoidea vix 5 cm. longa, ramis longissimis (forsitan 2-3 dm.)



Figs.1-3.—Type specimens of *Micropuntia*, collected near the United States Desert Experimental Range west of Milford, Utah, by Gordon Marsh in November, 1945 (No. 3 collected in Jan. 1946). From left to right: (1) *Micropuntia brachyrhopalica* Daston, (2) *Micropuntia Barkleyana* Daston, and (3) *Micropuntia spectatissima* Daston. Reduced 2/5.

Micropuntia Barkleyana sp. nov.

Praestat spinis ± complanatis omnibus sordide argentea-griseis, radialibus 4 vel 6 circa 1 cm. longis, centralibus 2 raro 4 circa 2½ mm. longis basi conspicue bulbosis, radice primaria ± 1 dm. longa superne sensim attenuata sub medio obconica.

Micropuntia spectatissima sp. nov.

Plantae humiles, ramis praestat cylindricis, 3-5 cm. longis circa 5 mm. crassis, areolis setaceis albis mollibus 2½ mm. longis, aculeis nullis vel 2-4 gracillimis griseo-albis 1 vel 2½ cm. longis, mammillis 1-1½ mm. longis crassisque opaco-brunneo-purpureis; fructo sicco globoso atque aculeis intense albis armato, radice primaria, pro 6 speciminibus observatis, ± 1 dm. longa et ± 2½ cm. crassa, sub medium radicibus numerosis iis demissis gracillimis usque ad 2-3 dm. longis onusta.

CHICAGO NATURAL HISTORY MUSEUM,
CHICAGO, ILL.

A New Species of Heterosporium Pathogenic on Young Chinook Salmon

Maxwell S. Doty[1] and Daniel W. Slater[2]

During the course of investigating the nature of diseases affecting chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), at Coleman Fisheries Station, Anderson, California, the junior author isolated from kidney mycoses of yearlings what seems to be the causative organism of one disease, the following previously unknown species.

Heterosporium tshawytschae sp. nov.

Mycelium laminas fuscas hyphis subfuscis immersis atque hyalinis divaricatis compositas efformans; hyphae 1.5-4μ diam.; cellulae plerumque 16-20μ longae; conidiophora hyphis vegetativis similia; conidiosporae singulae alternato ordine vel irregulariter collocatae, sparse subtuberculatae, maturitate fuscae et plerumque triseptatae, elliptico-oblanceolatae in parte inferiore erostratae, saepe minute truncatae, apice hemisphaerico, quadriloculares, 14-20μ longae, 4-6μ latae.

Mycelium forming dark brown plaques of immersed pale-brown hyphae with hyaline hyphae erect from the surface and immersed in the medium at the margin of the growing colony; hyphae cylindrical, smooth walled, irregular in size (1.5) 2-4μ in diameter, sometimes a bit irregularly swollen, branching at between 40° and 90° from the main axes; cells very variable in length but often 16 to 20μ, with the ends often somewhat swollen and constricted at the septa; conidiophores arising from the surface of the hyphal mass in culture as loose wefts of mycelium from which the spores usually arise as apedicellate lateral branches, or the spores may arise directly from surface mycelium not differing in appearance from the other hyaline or pale-brown hyphae; conidiospores sparsely low-tuberculate, becoming brown and almost always three-septate at maturity, elliptic-oblanceolate in outline with no trace of a rostrum at the base though often minutely truncate there, locules regular in size and cylindrical or slightly swollen, particularly at the distal end, apex hemispherical, produced solitarily and laterally, alternately or irregularly on the conidiophores, quadrilocular, at maturity 14-20 x 4-6μ.

The type, consisting of slides of cultured sporogenous mycelium and paraffin-sectioned material from infected fish organs, is deposited in the Dudley Herbarium of Stanford University (number 306407). Subcultures have been distributed to the Farlow Herbarium at Harvard University, to the University of California herbarium, to Dr. Gladys E. Baker of Vassar College,

1 School of Biology, Stanford University, California. Present address: Northwestern University, Evanston, Ill.

2 U. S. Fish and Wildlife Service, Coleman Fisheries Station, Anderson, California.

to Dr. J. Émile Jacques at the Montreal Botanical Garden, and to the American Type Culture Collection (No. 9915), Georgetown University School of Medicine, Washington 7, D. C.

Among the known species of the genus *Heterosporium* this species[3] is distinct by virtue of the small sparsely-scattered warts on the spore surfaces, and by the almost constant production of quadrilocular spores which are small for the genus. Repeated transfers on various solid and liquid media have little effect on the morphological characteristics. When characteristic the colonies

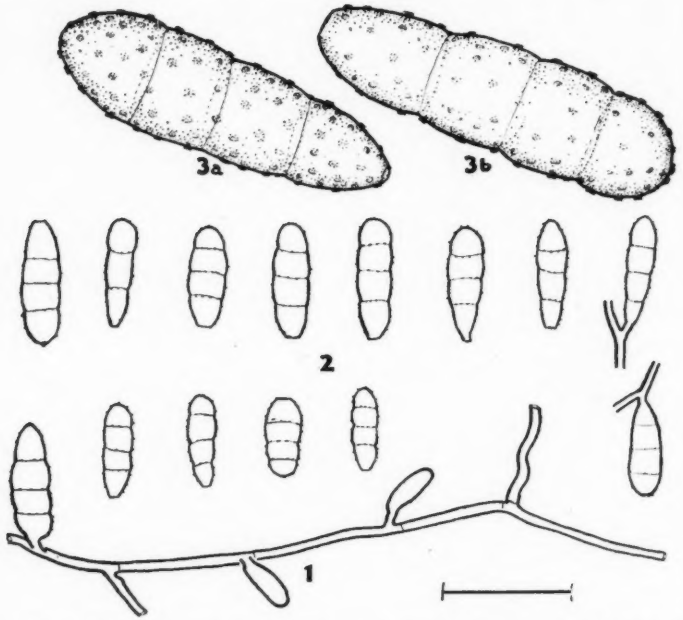


Fig. 1.—A very narrow conidiospore-bearing mycelial fragment. Fig. 2.—Camera lucida outline drawings to illustrate many of the variations in spore form. Fig. 3.—Drawings of the roughest and broadest spores on a very large scale to show proportion of surface ornamentation. All but figure 3 may be compared with the 20μ scale drawn below figure 1.

are lumpy and form dark brown stromata in the surface of the agar or spherical colonies with dark centers in liquid media. The aerial and first spore-producing hyphae appear as gray intertwined erect tufts on the surface of colonies usually not less than one week old. No specific growth requirements have been found.

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3 The authors are indebted to Dr. Émile Jacques for a confirmation of their comparison of this organism with other members of the genus.

This is the first record of this or any other[4] type of fungus as a deep mycosis in fish and the first record, insofar as the authors are aware, of this genus as a pathogen on animals of any sort. Preliminary studies show that the first parts of the kidney to be attacked are the mesonephric tubules, then the insterstitial granulopoietic tissue, and finally the Malpighian bodies themselves. In aggravated cases portions of the kidneys are entirely destroyed. The fungus is usually localized in two or three foci in the posterior half of the kidney as though it had entered through the mesonephric ducts from the cloaca. The importance of the fungus as a fish pathogen is thought to be slight. The microscopically-observed incidence of infection was less than one per cent, and all attempts to produce infections experimentally have failed.

There is the possibility that the infections originated from infected plant material in the water since on plants this genus of fungi is a common weak pathogen. Comparison of this species with the species of *Heterosporium* known in the area has, as yet, yielded no similar fungus. The fungus was isolated from two different fingerlings and observed in about 40 more. In addition, it is the only fungus isolated in about fifty cultures made in an identical manner from the kidneys of the same lot of chinook fingerlings. It has never appeared as a contaminant in any of our cultures. What is still more clearly conclusive that this is the causative organism is that the mycelium in culture has the same size, branching, color, and general appearance as in the fish kidney with the exception that no spores are to be found in the animal host.

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4 Except for one perhaps questionable record: Agersborg, H. P. K., Salient problems in the artificial rearing of salmonoid fishes, etc. Amer. Fish Soc. Trans. **63**:240-250. 1933.

List of Myriapoda Taken in Champaign County, Illinois, During the Fall and Winter of 1944-45[1]

Janet L. C. Rapp

These myriapods were collected on trips taken in connection with the author's thesis problem[2] dealing with the habitats of insects in their hibernating state. The actual territory studied, lying within an approximate eleven mile radius of Urbana, included as stations the six communities of Bondville, Champaign, Mahomet, Mayview, St. Joseph, and Urbana. The myriapods, which were not covered in the thesis, were for the most part taken with the use of a Jacot[3] apparatus, a modification of the one proposed by Berlese. Different types of litter, collected and bagged in the field, were brought to the laboratory and placed in the apparatus. Essentially this consisted of a large funnel of sheet steel or copper with a sieve at the bottom. A 300 watt bulb was suspended within an inch of the litter to drive the animals downward by dry heat. At the base of the funnel a beaker of 70 percent alcohol was placed to catch the specimens as they came through the sieve.

The myriapods were determined by Dr. R. V. Chamberlin, Department of Biology, University of Utah.

The species are arranged alphabetically under the two orders collected:

Diplopoda

Aniulus rugosus (Bollman)—Champaign, Oct. 15, 1944, M, F, Oct. 21, 1944, F, Illinois Central Railroad right-of-way; St. Joseph, Nov. 12, 1944, along the banks of the Salt Fork River.

Pseudopolydesmus euthetus Chamberlin—Champaign, Oct. 21, 1944, 2, Illinois Central Railroad right-of-way.

Schendyla nemorensis (Koch)—Champaign, Oct. 21, 1944, along the right-of-way of the Illinois Central Railroad.

Scytonotus granulatus (Say)—Champaign, Oct. 15, 1944, along the Illinois Central Railroad tracks; Urbana, Oct. 22, 1944, along the west branch of the Salt Fork River; St. Joseph, Nov. 12, 1944, banks of the Salt Fork River.

Chilopoda

Geophilus rubens Say—Mahomet, Mar. 4, 1945, loose dirt with a few leaves from open ground under sycamore tree.

Linotaenia fulva (Sager)—Urbana, Feb. 18, 1945, log pried up on top of hill; tree about 35 feet long in addition to stump; sample consisted of debris and soil; Urbana, Feb. 25, 1945, broken pieces of old log.

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1 Contribution No. 262 from the Entomology Department of the University of Illinois, Urbana, Illinois.

2 "Insect Hibernation Studies in Champaign County, Illinois During the Winter of 1944-45." Unpublished manuscript in the University of Illinois.

3 Jacot, A. P. 1936—Soil Structure and Soil Biology. Ecology **17**:359-379.

Lithobius forficatus (Linné)—Urbana, Oct. 22, 1944, 2, right-of-way of the Illinois Central Railroad; Mayview, Dec. 3, 1944, West Branch of the Salt Fork River.

Nadabius sp.—Bondville, Oct. 24, 1944, banks of the Kaskaska River; Mahomet, Nov. 25, 1944, immature, banks of the Sycamore River; Mar. 4, 1945, loose dirt with a few leaves from open ground under sycamore tree.

N. iowensis (Meinert)—Champaign, Oct. 15, 1944, along right-of-way of Illinois Central Railroad; St. Joseph, Nov. 12, 1944, banks of the Salt Fork River; Urbana, Feb. 18, 1945, immature, woody area on south side of hill, under pried-up log, material not frozen, mostly debris with soil; soil and debris from under pried-up log in valley; young, soil and debris from pried-up log on crest of hill; Feb. 25, 1945, F, leaves from sheltered hollow in ground; Mahomet, Mar. 4, 1945, young, loose dirt with a few leaves from open ground under sycamore.

Physobius rappi Chamberlin—Mahomet, Mar. 4, 1945, loose dirt with a few leaves from open ground under sycamore tree.

Pokabius bilabiatus (Wood)—FF, St. Joseph, Feb. 11, 1945, loose leaves and debris from stream; somewhat protected by willow seedlings.

Tidabius plesius Chamberlin—Urbana, Feb. 25, F, log pried up on top of hill, sample consisted of debris and soil.

A List of Thysanoptera Known to Occur in Indiana

C. C. Blickenstaff

Although about 75 species of Thysanoptera are known from the four bordering states, including at least 70 recorded from Illinois alone, only 15 species have been previously reported from Indiana. Russel in 1912 recorded *Aeolothrips bicolor* Hines as occurring in Indiana. Watson in 1923 cited only three species—*Frankliniella tenuicornis* (Uzel), *Limothrips cerealium* Halliday, and *Neoheegeria verbasci* (Osborn)— actually known from Indiana, although a fourth, *Haplothrips leucanthemi* (Schrank), was listed as present in all the states, and a fifth, *Heliothrips haemorrhoidalis* (Bauche), as common in greenhouses in the northern states. Hood added *Sericothrips apicalis* Hood to the list in 1927, and Davis reported *Taeniothrips simplex* Morison for Indiana in 1932. Bailey in his list of injurious thrips of the United States, published in 1940, listed seven additional species for Indiana, but did not give the original records.

During 1942 and 1943 the author collected and studied thrips during the preparation of an undergraduate thesis.[1] The following list condensed from the thesis is based upon records, in literature, specimens collected by the author in 1942 and 1943, and other specimens from Indiana in the Entomological Collections of Purdue University.

The list includes 34 species of which 18 are recorded from the state for the first time. Many species that certainly occur in Indiana as indicated by records of their distribution in neighboring states have not been collected within the state to the knowledge of the author and are not recorded here.

In the following records initials are used to designate the collector as follows: JJD—J. J. Davis, GEG—G. E. Gould, CCA—C. C. Alexander, GC—G. Cummins, JMA—J. M. Amos, and CCB—C. C. Blickenstaff.

Appreciation is extended to Dr. H. O. Deay, Dr. B. E. Montgomery, and Prof. J. J. Davis of Purdue University for their guidance in this study.

Most of the determinations were checked by J. C. Crawford of the U. S. National Museum; many of the specimens collected by J. J. Davis had been checked by J. D. Hood.

Species marked with an asterisk are those recorded from Indiana for the first time.

List of Species

Suborder Terebrantia

Aeolothripidae

*1. *Aeolothrips fasciatus* (Linn.)—Lafayette, July 23, 1942, field corn. CCB; Royal Center, June 16, 1942, wild mustard, CCB.

2. *Aeolothrips bicolor* Hinds.—Knox, onion (Russel, 1912); Lafayette, August 18, 1911, pentstemon, JJD.

[1] Prepared under the direction of Professors H. O. Deay and B. Elwood Montgomery, and submitted to the faculty of Purdue University in partial fulfillment of the requirements for the degree of Bachelor of Science in Agriculture, August, 1943. Records from this thesis are published by permission of the Dean of the School of Agriculture.

Aeolothrips sp.—Lafayette, May 6, 1943, dandelion, CCB. Nymphs of undetermined species of Aeolothripidae were collected from alfalfa, bluegrass, and *Abies concolor* at Lafayette, June 7 and 9, 1943, CCB.

THRIPIDAE

3. *Chirothrips manicatus* Haliday. The manicate thrips.—Lafayette, June 7, 1943, bluegrass, CCB.

4. *Limothrips cerealium* Haliday. The cereal thrips.—Indiana (Watson, 1923); Franklin, June 12, 1911, wheat, JJD; Washington, April 24, 1921, wheat, JJD; Lafayette, July 23, 1942, elderberry, CCB.

5. *Sericothrips apicalis* Hood.—Described as a new species by Hood (1927) from specimens taken at Knox and Ober, July 16, and August 1, 1914, on *Stachys palustris* (a nettle), by M. M. High.

6. *Sericothrips variabilis* (Beach).—The variable thrips. Indiana (Bailey, 1940); Lafayette, October 9, 1911, leaf gall of black locust, JJD; Lafayette, October 10, 1942, in flight; May and June, 1943, foliage of elm and poplar, CCB.

*7. *Sericothrips nublipennis* Hood.—Lafayette, June 2, 1943, green galls of ash tree leaves, CCB.

8. *Dendrothrips ornatus* (Jablon). The privet thrips.—Indiana (Bailey, 1940); Lafayette, June 9, and August, 1943, *Ligustrum ibota regalianum*, CCB.

9. *Heliothrips haemorrhoidalis* (Bouché). The greenhouse thrips.—Indiana greenhouses, chrysanthemum (Davis, 1926); Indiana (Bailey, 1940). Several greenhouses in and near Lafayette were examined during 1942 and 1943 for this reportedly common species but it was not found.

10. *Hercinothrips femoralis* (Reuter). The sugar-beet thrips.—Indiana (Bailey, 1940); Lafayette, greenhouses, December, 1932, JMA; January, 1933, and September, 1933, GEG; February, 1938, CCA; *Amaryllis*, aster, *Bryophyllum*, cocklebur, Russian dandelion, eggplant, *Freesia refracta alba*, marigold, mint, potato, peach seedling, rattle-snake master, tomato, tobacco, and sweet-potato in greenhouses throughout the years of 1942 and 1943, CCB.

*11. *Scolothrips sexmaculatus* (Pergande).—Lafayette, June 9, 1943, *Juniperus sabina*, CCB.

12. *Frankliniella tritici* (Fitch). The common flower thrips.—Indiana (Bailey, 1940); Fort Wayne, July 18, 1933, carrot seedlings, GEG; Lafayette, May 6, 1921, apple, May 18, 1931, Weigelia flowers, JJD; Lafayette, October, 1936, gladiolus, CCA; Lafayette, spring, summer, and fall of 1942 and 1943, alfalfa, African violet, *Amaryllis*, ash tree, corn lily, catnip, calla lily, carrot, wild cherry, mammoth clover, white clover, field daisy, dandelion, elderberry, elm leaf, *Euonymus europus*, field bindweed, *Fuchsia*, gladiolus, grass, hollyhock, lilac, mustard, *Philadelphus* sp., red sorrel, *Robinia hispida*, rose, sweet-pea, spirea, *Viburnum* sp., wheat, *Weigela*, and *Yucca*, CCB. This species is very common and is found in the flowers of nearly all plants.

*13. *Frankliniella tritici varicorne* Bagnall.—Royal Center, June 21, 1942, hollyhock flowers and corn lily blossoms, CCB.

14. *Frankliniella fusca* (Hinds). The tobacco thrips.—Franklin, June 12, 1911, wheat, JJD; Lafayette, June 25, 1912, corn, JJD; October, 1942 and May and June, 1943, alfalfa, alsike clover, bluegrass, and broad-leafed plantain, CCB.

15. *Frankliniella tenuicornis* (Uzel).—Indiana (Watson, 1923), under the name *F. nervosa* (Uzel); Lafayette, June and July, 1942 and 1943, wheat, field corn, and *Robinia hispida*, CCB.

16. *Taeniothrips simplex* (Morrison). The gladiolus thrips.—Reported by Davis (1932, 1934, 1936) as causing considerable damage, being generally distributed in Indiana (Bailey, 1940); Lafayette, 1936, gladiolus bulbs and flowers, CCA; Lafayette, winter and summer, 1942 and 1943, gladiolus bulbs and flowers, CCB.

17. *Thrips tabaci* Lindeman. The onion thrips.—Reported in Indiana by Davis as a very troublesome pest of chrysanthemums during May, also on feverfew and carnations (1926), damaging garden crops in northern Indiana in June and July (1930), damaging pompoms and cyclamen in a New Albany greenhouse in January, and

threatening onion fields in June (1932), destructive to onions in July, destroying 30 acres of seedling carrots at Fort Wayne in July (1933), very abundant in northern Indiana in June and July (1934), and damaging onions at Ligonier in June (1937). Lafayette, throughout 1942 and 1943, tomato, onion, wheat, chrysanthemum, *Ageratum*, sweet-pea, yucca bloom, rose buds, *Freesia*, jonquil bloom, bean, cosmos, *Phlox*, *Anchusa*, peach leaves, pepper, gladiolus, and *Lantana*, CCB. Most collections were made in greenhouses. Specimens were also taken in May, 1943 from cauliflower which had been shipped to Lafayette from California.

*18. *Thrips spinosus* Morgan.—Lafayette, June 25, 1912, corn, JJD.

*19. *Thrips nigropilosus* Uzel. The chrysanthemum thrips.—Lafayette, April 3, 1943, chrysanthemum and eggplant, CCB.

*20. *Thrips trehernei* Pr.—Lafayette, June, 1943, hollyhock flowers and dandelion bloom, CCB.

*21. *Microcephalothrips abdominalis* (Crawford). The Compositae thrips.—Lafayette, March, April and May of 1943, dandelion, field daisy and catnip, CCB.

22. *Anaphothrips obscurus* (Mull.). The northern or eastern grass thrips.—Indiana (Bailey, 1940); Franklin, June 12, 1911, wheat, JJD; Lafayette, June and July of 1943, wheat and corn, CCB.

*23. *Aptinothrips rufus* (Gmelin).—Fenton, March 24, 1916, turf, JJD; Lafayette, June 2 and 7, 1943, bluegrass and alfalfa, CCB.

Suborder TUBULLIFERA

PHLOEOTHRIPIDAE

*24. *Hoplothrips karnyi* (Hood).—In the collection at Purdue without collection data. It was checked by Crawford as probably being this species.

*25. *Hoplothrips major* (Hood).—Lafayette, November 18, 1931, apple tree, GC.

26. *Liothrips vaneeckei* Pr. The lily thrips.—Indiana (Bailey, 1940).

*27. *Liothrips citricornis* (Hood).—Lafayette, May 19, 1913, hickory, JJD.

*28. *Bagnelliella yuccae* (Hinds).—Royal Center, July 16, 1942, yucca blossom, CCB.

29. *Haplothrips leucanthemi* (Schrank). The statice thrips.—There are no specific Indiana records for this species but Watson (1923) recorded it as occurring in "all U. S.," and Bailey (1940) recorded it from 16 other states scattered throughout the United States.

*30. *Haplothrips flavipes* (Jones).—Lafayette, October 10, 1942, bark of an apple tree, CCB.

31. *Neoheegeria verbasci* (Osborn). The mullein thrips.—Indiana (Watson, 1923); Lafayette, April 5 and October 10, 1942, and February 21, 1943, mullein; June 2, 1943, green galls of ash tree leaves, and on pig hickory leaves, CCB.

*32. *Hoplothrips angusticeps* (Hood).—Staunton, March 1, 1921, fungus, JJD.

*33. *Leptothrips mali* (Fitch). The black hunter thrips.—Bloomington, August 11, 1911, tulip tree; Lafayette, April 12, 1921, in flight, May 6, 1921, apple, JJD; Lafayette, June 9, 1943, *Euonymus europus* bloom, CCB.

*34. *Elaphrothrips armatus* (Hood).—Lafayette, June 2, 1943, weed sweepings, CCB.

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New and Little Known Dolichopodidae from Indiana (Diptera)[1]

F. C. Harmston and G. F. Knowlton[2]

This report includes a key to the four species of flies in the genus *Teuchophorus* known to occur in North America; one of these is described as new. Also an apparently new *Dolichopus* is described, together with collection notes and a description of the previously undescribed male of *D. aethiops* Van D.

Teuchophorus condylus n. sp.

Male.—Length, 1.3 mm.; length of wing, 1.5 mm. Ground color of face dark blue, covered with grayish-white pollen. Front metallic, steel-blue, somewhat dulled with white pollen along the orbits. Lower orbital cilia white; the upper cilia are black and descend to the middle of the eye. Antennae black; third joint rounded at apex, densely pubescent. Arista dorsal, long and tapering, pubescent, inserted at base of third joint. Palpi black, pubescent, bristly at tip.

Dorsum of thorax and the scutellum blue-green, lightly dusted with whitish pollen; pleurae dulled with grayish pollen. Abdomen metallic green, the lateral portions with bronze reflections, the bristles short, black. Hypopygium small, black; outer lamellae minute, black, oval, clothed with delicate pale hairs; inner appendages yellow, directed backward.

Coxae and legs yellow; all tarsi infuscated from near the tip of second joint as are also the posterior femora on upper apical portion. Fore and middle coxae with delicate pale hairs on anterior surface and a few black bristles at tip. Fore femora without noticeable bristles. Middle femora with a prominent black bristle near the base on lower edge, this bristle being nearly twice as long as the width of femora; slightly nearer to the base of middle femora is another, smaller bristle placed in line with the larger one. Hind femora with a few delicate pale hairs along lower edge and a row of black bristles on upper basal half. Fore tibiae of ordinary structure, without noticeable bristles. Middle tibiae with two prominent black bristles near the middle on anterior surface. Hind tibiae slightly thickened, bearing a peculiar black, spur-like appendage near the basal third on inner side, the posterior edge with a row of about eight short, sharp bristles on apical half and a strong bristle on inner edge near the apex. First joint of fore tarsi bearing a row of short bristles on plantar surface. Middle and hind tarsi of plain structure. Joints of fore tarsi as 20-7-6-5-6; of mid tarsi as 23-9-7-6-6; of hind tarsi as 16-16-9-7-5. Halteres yellow, calypters yellow with black cilia.

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1 Contribution from Zoology and Entomology Department, Utah State Agricultural College.

2 Graduate student and professor, respectively.

Wings gray, hyaline; costa not thickened; third and fourth veins parallel from beyond the cross-vein, the fourth vein ending in the wing tip; cross-vein oblique, one-half the length of last section of fifth vein.

Described from one male taken at Terre Haute, Indiana, September 12, 1943 by F. C. Harmston. Holotype to be deposited in the U. S. National Museum.

Differentia.—*T. condylus* n. sp. is the fourth species of *Teuchophorus* to be described from North America. It resembles *diminucosta*, from Utah, in general appearance, from which it is readily separated by the difference in structure of the spur-like appendage on posterior tibiae. In *condylus* the appendage is but slightly longer than the width of tibiae and tapers to a rather sharp point; in *diminucosta* the appendage is nearly three times as long as the width of tibia, is strongly sinuous and expanded at tip.

The following key will serve to separate the four species of *Teuchophorus* known to occur in North America.

1. Costa not thickened on first portion 2
   Costa thickened on first portion; this thickened area is black, tapers rapidly and ends midway between the tips of first and second veins 3
2. Spur-like appendage on inner side of posterior tibia, near basal third, sharp at tip, nearly straight, slightly longer than the width of tibia ..... *condylus* n. sp.
   Spur-like appendage nearly three times as long as width of tibia, strongly sinuous and expanded at tip ..... *diminucosta* ....H. & K.
3. Middle and hind coxae black; all femora black except narrowly at tips, or the posterior femora may be yellowish below at extreme base ..... *utahensis* H. & K.
   Middle and hind coxae light yellow; all femora yellow, except for a slight infuscation on hind pair at apex on upper side ..... *clavigerellus* Whlr.

Dolichopus indianus n. sp.

Male.—Length, 4.5 mm.; of wing, 4.2 mm. Face silvery pollinose, of moderate width, somewhat narrowed on lower portion where its width is slightly less than the distance between the tips of 3rd and 4th wing veins. Front dark, metallic green, lightly dusted with whitish pollen along the orbits. Palpi brown, their tips with thin white pollen, their surfaces with minute black hairs. Antennae black; third joint large, nearly 1½ times as long as wide, the lower edge evenly rounded, obliquely pointed at tip. Arista scarcely longer than antennae, inserted at the apical fourth of upper edge. Upper orbital cilia black; lateral and inferior cilia white.

Dorsum of thorax dark, metallic green, very lightly dusted with grayish pollen and with a narrow, dull-bronze, median vitta; pleurae concolorous with the dorsum, but the pollen much heavier, nearly obscuring the ground color. Abdomen bright metallic green, the incisures and dorsum with bronze reflections. Hypopygium black; lamellae white with narrow black border, rather large, rounded, about as wide as long, the apical portion jagged and bristly.

Fore coxae yellow, the outer surface black nearly to the middle, their anterior surfaces with minute black hairs except on the outer basal portion where the delicate hairs are pale; bristles at tip of fore coxae black. Middle and hind

coxae black, narrowly yellow at tips. Femora yellow, the posterior pair black at tip on upper surface; middle and hind femora each with one preapical bristle. Posterior femora not ciliate below, but with a row of delicate pale hairs on lower, inner edge which are perceptible only at high magnification. Tibiae yellow, the posterior pair slightly thickened and black on apical one-third; the dark color extends as a brown stripe to the base of tibia on inner edge. Middle tibia with a single bristle on lower surface inserted near the apical one-fourth. Fore tarsi black from tip of first joint; middle tarsi black from middle of first joint which is without a bristle on upper edge; hind tarsi wholly black, somewhat thickened. Joints of fore tarsi as 20-8-6-4-5; of middle tarsi as 30-14-11-8-6; of hind tarsi as 20-20-15-8-6. Halteres, calypters and their cilia, yellow.

Wings grayish hyaline; costa not enlarged at tip of first vein; fourth vein bent just before its middle, from which point it converges gradually toward tip of third vein; anal angle not prominent, the wing narrowed toward base.

Described from twelve males from Indianapolis, Indiana, collected March 21, 1943 by F. C. Harmston. Holotype to be deposited in the U. S. National Museum; paratypes in the Utah Agricultural Experiment Station insect collection and in the collection of the senior author.

Differentia.—*Dolichopus indianus* n. sp. traces to *D. fucatus* Van D., or possibly to *D. gladius* Van D. in the Van Duzee and Curran Key to Nearctic Dolichops (American Mus. Novitates, No. 683, 1934). *D. indianus* is readily distinguishable from *fucatus* by the form of antennae whose third joint is elongate-oval, 1½ times as long as wide, whereas the third antennal joint in *fucatus* is orbicular, scarcely longer than wide. The costal vein of *gladius* has a prominent knot-like swelling at the tip of the first vein, distinguishing it from *indianus* which has the costa plain.

DOLICHOPUS AETHIOPS Van Duzee

This species was described by Van Duzee in 1916, Bulletin 116, U. S. National Museum, from a single female taken at Lafayette, Indiana. Apparently the male has never been described so we give here a description of the male together with notes concerning the species.

The female of *aethiops* is incorrectly placed in the two keys to North American Dolichopus, (Bulletin 116, U. S. National Museum, 1916; and American Museum Novitates, No. 684, 1934) which state that the middle basitarsus is yellow at base. However, in his description of the female, Van Duzee gives the color of legs as black which agrees with the color of legs in all nine females now at hand.

Male.—Length, 5.4 mm.; length of wing, 5.5 mm. Face yellowish-brown, wide for a male, the sides nearly parallel, yet slightly narrowed on lower portion where there is a pronounced convexity; its width at narrowest portion slightly exceeds the distance between the tip of third and fourth wing veins. Front dull, metallic green, almost black, lightly brownish pollinose. Palpi black, with minute black hairs on their anterior surfaces and a prominent, larger black hair at tip, the apices silvery pollinose. Proboscis black. Antennae black; third

joint scarcely longer than wide, evenly rounded on lower edge, obtusely pointed. Arista inserted near the middle of third joint. Lower orbital cilia white; the upper black cilia descend about one-third the eye height.

Dorsum of thorax so thickly brownish pollinose that the dull, greenish-bronze ground color is barely perceptible; a pair of narrow, dark-brown vittae flank the small acrostichal bristles; each of the large thoracic bristles arise from a darker spot. Pleurae black, dusted with grayish pollen. Dorsum of abdomen and the incisures red-bronze, the lateral portions metallic green, lightly grayish pollinose. Hypopygium black, lightly dusted with gray pollen; the lamellae nearly oval, white, shading into yellow near the base, with moderately wide black border, the apical portion jagged and bristly.

Coxae and all of legs wholly black. Fore coxae lightly whitish pollinose; the anterior surfaces with small black hairs and the usual black bristles at tip. Middle tibiae with a prominent bristle on lower surface, situated slightly beyond the middle. Middle basitarsus without a bristle on upper surface. Middle and posterior femora each with a single preapical bristle, the latter with delicate cilia on lower, inner edge; these cilia appear pale in some lights, dark in others, their length equals one-third the width of femora. Joints of fore tarsi as 20-10-8-5-5; of middle tarsi as 25-15-10-8-6; of hind tarsi as 22-22-15-10-8. Halteres and calypters yellow, the latter with black cilia.

Wings grayish hyaline, with a prominent, jet black spot near the apex on the posterior margin; costa with an elongate enlargement at the tip of first vein; anal angle evenly rounded.

Description made from neallotype male collected near Indianapolis, Indiana, March 21, 1943 by F. C. Harmston. Thirteen additional males and nine females were taken at the same place between the above date and the fore part of May. All were found resting on wet rocks along a small stream in a densely wooded area just north of Fall Creek, near the Ft. Harrison Military Reservation. The specimens were extremely active and considerable difficulty was experienced in collecting them by means of an ordinary insect net. The species is an early season form and apparently is limited to particular environments as it was not observed after the fore part of May nor in any locality other than that listed, even though efforts were made to collect specimens in other, favorable-appearing localities in the Indianapolis area.

Differentia.—This remarkable species appears at first sight to be identical to *jaquesi* H. & K. Both are large, predominately black in color and possess the black spot at the wing tip. They are readily separated, however, by the difference in color of orbital cilia, these being wholly black in *jaquesi*, while in *aethiops* the lower cilia are white. The neallotype male will be deposited in the U. S. National Museum; other specimens are in the Utah Agricultural Experiment Station insect collection and in the collection of the senior author.

Age and Growth of the Rustyside Sucker, Thoburnia rhothoeca (Thoburn)

Edward C. Raney and Ernest A. Lachner

The rustyside sucker, *Thoburnia rhothoeca* (Thoburn), has been known to taxonomists for some fifty years yet almost nothing has been published on its life history. It is a small species that inhabits the small mountain streams of the upper James River, Potomac River, and Kanawha River systems in western Virginia and West Virginia. It prefers the swifter parts of rapidly flowing streams where it is often abundant and is structurally modified for life in such a habitat. Among the adaptations pointed out by Hubbs (1930: 45), the head is "small, convex, decurved; the skull thick, with obliterated fontanelle." In adults the two chambered airbladder is much reduced in size. This sucker is of little or no economic importance as human food since it probably seldom exceeds seven inches in total length. It might possibly be of some use as bait fish and may be utilized to some extent in nature as forage by game fish.

The specimens studied came from varied habitats at several localities, listed in detail in Table 1. In the spring of the year when our only observations were made, it was most common in the riffles of medium streams 50 to 100 feet wide where the bottom varies from bed rock to boulders, rubble, and large gravel. Although it occurs in moderately sluggish streams it is found in the swifter portions and is not often seen in the deeper pools. It was commonly associated with the following species, which are listed below in the order of their frequency of occurrence: *Notropis cornutus cornutus, Boleosoma longimanum, Catonotus flabellaris, Schilbeodes marginatus marginatus, Rhinichthys cataractae, Boleosoma nigrum, Rhinichthys atratulus atratulus, Nocomis leptocephalus, Clinostomus vandoisulus* and *Hypentelium nigricans*. Fourteen other species were also found associated with it at three or fewer localities. It should be noted that most of the above species are typically found in the swifter portions of streams they inhabit.

Actual spawning behavior was not noted although many ripe males in full breeding color were found in the same area with ripe females. These observations were made when the water temperatures varied from 56° to 61° F. during the last few days of March and the first week in April, 1940. At the same date the following spring it was much colder due to unseasonal snows, the water temperatures ran from 44° to 50° F., and no ripe *Thoburnia* were seen.

The sexes are easy to distinguish in the breeding season on the basis of color and body shape; the females are swollen. At other times probably the best character to use is the combination of longer dorsal and ventral fins in the male. The sexual dimorphism is given in some detail in Table 2. The distribu-

TABLE 1.—Collections from the Upper James River System, Virginia, used in Age-Growth Study of *Thoburnia rhothoeca*.

Locality	Date	Immature[1]	♂	♀	Total
Nelson Co., Tye R., 2 mi. NW. of Roseland	Apr. 7, 1940	..	26	23	49
Albemarle Co., Mechums R., 3 mi. W. of Ivy	Apr. 7, 1940	..	5	4	9
Rockbridge Co., Buffalo Cr., 4.5 mi. SW. of Lexington	Mar. 30, 1940	..	4	3	7
Rockbridge Co., Belle Cove Branch, trib. of North R., 4 mi. S. of Buena Vista	Oct. 10, 1940	9	..	..	9
Rockbridge Co., trib. of North R., 5 mi. W. of Lexington	Mar. 30, 1940	..	19	22	41
Botetourt Co., Catawba Cr., 2 mi. N. of Fincastle	Mar. 31, 1940	..	9	32	41
Alleghany Co., Pounding Mill Cr., 1.5 mi. SE. of Covington	Apr. 5, 1941	..	9	13	22
Highland Co., Jackson R. at Vanderpool	Apr. 5, 1941	10	11	15	36
Total		19	83	112	214

[1] Specimens in their first year which could not be readily sexed with a binocular microscope.

tion of the breeding tubercles described in Table 2 is substantially the same as that of the hog sucker, *Hypentelium nigricans*, and the common white sucker, *Catostomus c. commersonnii*.

In order to obtain a general idea of fecundity, the ovaries were removed from three females and the eggs were counted. Near the spawning time in late March and early April the ovaries almost fill the abdominal cavity dorsad of the long alimentary canal. The right ovary is longer than the left and contains more eggs. The results of the egg count follow: total length 108 mm., right ovary 483, left ovary 259, total, 742; total length 112 mm., right ovary 694, left ovary 496, total 1190; total length 144 mm., right ovary 1093, left ovary 656, total 1749. Large specimens of common white sucker, *Catostomus c. commersonnii*, have many more eggs as reported by Raney and Webster (1942: 147). No data are available from common white suckers of comparable sizes. It was noted incidentally that the ratio of total length to length of the alimentary canal in each of the above mentioned *Thoburnia* was 2.1, 2.2, and 2.3 respectively.

A study of the scales of a large collection from one locality, consisting of specimens from very small to mature adults, revealed that the ages could be determined for this species. The scale method has been, in our opinion, validated for several species of suckers by a number of workers. The annulus appears most pronounced on the posterior lateral field as it cuts across one or more previously formed circuli. It may also be observed on the anterior and lateral fields. Banding caused by the wide spaced circuli of early summer as

TABLE 2.—Sexual dimorphism in adult *Thoburnia rhothoeca*.

	Male	Female
Lateral band in breeding fish	Narrow red lateral band prominent between dark blotches of extended saddles. Band about one quarter inch wide in five inch males.	Narrow brown lateral band.
Dorsal fin (in specimens over 50 mm. total length (ten dorsal rays).	Longer; distance from origin of dorsal to end of most posterior dorsal ray into standard length less than 3.8 times, usually 3.6; the difference is due to the prolongation of the last four or five rays rather than an increased number of rays.	Shorter; distance in standard length 4.1 times or more, usually 4.2 times.
Ventral fin	Longer; almost reaching anterior base of anal papilla.	Shorter; not nearly reaching anterior base of anal papilla.
Anal papillae	Less well developed; in ventral view, short and broad, about as long as broad; with several longitudinal grooves especially near posterior edge.	Much better developed; much longer than wide; more tubular in shape and with few or no longitudinal grooves near posterior edge.
Pearl organs on fins in breeding fish	Much larger; well developed on anal fin with a row of strong tubercles laterad of each ray; less strong on caudal fin but tending to cover fin, and to form lines laterad of the rays, those on lower half of fin somewhat larger than those on upper half; underside of ventral fins with very small tubercles arranged in rows along rays and best developed on posterior half of fin.	Weaker although present; on anal fin about 3 rows of three or four tubercles laterad of the rays in the middle of the fin; none observed on caudal or ventral fin.
Pearl organs on body	Best developed, though quite small on the posterior half of the body near the anal fin and on the underside of the caudal peduncle; minute over the head and dorsum anterior to the dorsal fin; in all cases tending to develop on the edge of each scale.	In general less well developed; small tubercles on edge of scales posteriorly near anal fin; also present on back in front of dorsal and on head although less strongly developed.

TABLE 3.—Length frequency distribution of two year old *Thoburnia rhothoeca* from four localities in the upper James River system, Virginia.

Locality		Tye R., 2 mi. NW. of Roseland		Pounding Mill Cr., 1.5 mi. SE. of Covington		Trib. of North R., 5 mi. W. of Lexington		Jackson R. at Vanderpool	
Date		Apr. 7, 1940		Apr. 5, 1941		Mar. 30, 1940		Apr. 5, 1941	
Sex		♂	♀	♂	♀	♂	♀	♂	♀
	50	..	..	..	..	1	..	..	..
Total	55	..	..	1	..	1	2	..	..
length	60	..	1	..	2	3	5	..	..
in	65	4	7	1	1	4	7	..	..
mm.	70	6	3	3	4	4	4	..	..
	75	7	4	1	2	1	..	..	3
	80	2	2	..	1	..	..	1	..
	85	2	..	2	..	..	..	5	..
	90	..	..	..	..	..	..	3	..
No.		21	17	8	10	14	18	9	3
Mean in mm.		75.2	71.6	73.6	71.4	66.3	64.7	86.9	74.0
Mean in inches		2.95	2.83	2.91	2.79	2.59	2.55	3.42	2.91

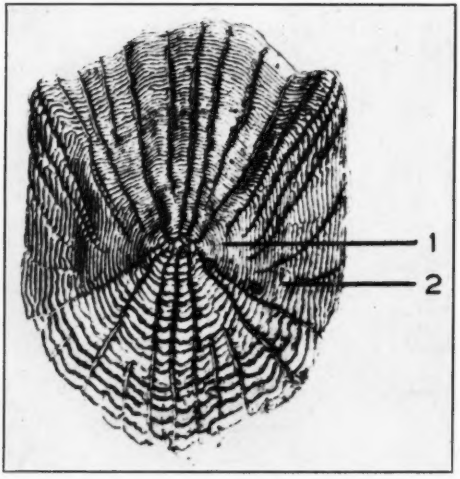

Fig. 1.—Scale of an adult male *Thoburnia rhothoeca*, 99 mm. total length, collected in Pounding Mill Creek, near Covington, Alleghany County, Virginia, on April 5, 1941. It has just completed its third winter.

contrasted with those spaced more closely late in the season is also helpful in determining age. The annulus is usually formed during the first half of April. These characteristics are shown in Figure 1.

The data on growth are summarized in Tables 3 and 4 and shown graphically in Figure 2. An examination of the data in Table 1 indicates an unbalanced sex ratio; there are 83 males and 112 females. On further analysis the sexes (as shown in tables 3 and 4) are about equal in number at the end of the second and third years. But if, as we believe, our data form a fairly representative sample of the populations as they occur in nature, the males tend to decrease in number as compared with females at the end of the fourth and

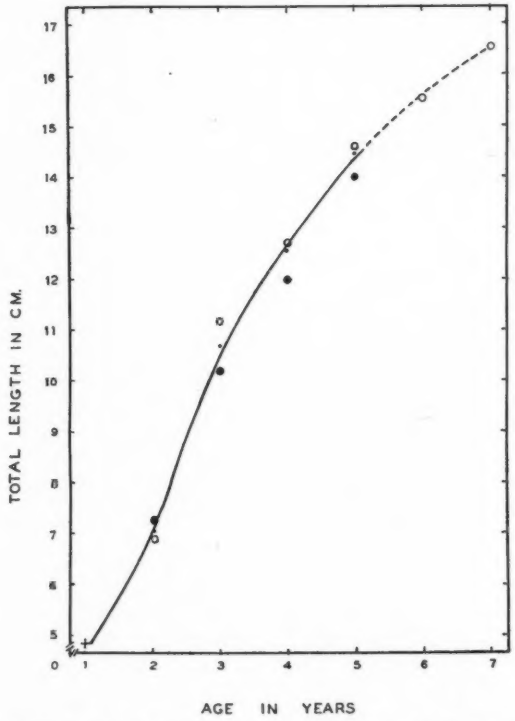

Fig. 2.—Growth curve of *Thoburnia rhothoeca* based on 214 specimens collected in the upper James River system, Virginia, from March 30 to April 7, 1940-41. See Table 3 for complete data. The curve has been drawn connecting the small solid dots which represent the mean total length of all specimens of an age group. The hollow circles mark the mean total length of females; the black circles represent the males; the plus sign indicates the mean of ten immature specimens one year old. The curve is broken at the upper end where very few specimens are available.

succeeding years. Our seining was done in the riffles where breeding is presumed to occur and males should normally be more common than females. The only representatives of the sixth and seventh year groups are females. There is probably not a significant difference in the length attained by males and females at least during their first four years. Most males are mature at two years and all spawn at three years. Females spawn for the first time when three years old.

Thoburn in the original description in Jordan and Evermann (1896: 182) gives the length as 3.5 to 5 inches. The largest seen by us is a female 6.6 inches total length and the longest male was 5.6 inches. Thus *Thoburnia* stands out not only as one of the smallest of eastern North American suckers but is also probably the most short lived.

TABLE 4.—Length frequencies for each age group of *Thoburnia rhothoeca* collected in the upper James River system, Virginia (see Table 1 for localities and dates) from March 30 to April 7, 1940-41.

Age		I*	I	II		III		IV		V		VI	VII
Sex		....	....	♂	♀	♂	♀	♂	♀	♂	♀	♀	♀
Total	30	4	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
length	35	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
in	40	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
mm.	45	1	6	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	50	.....	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.....
	55	.....	.....	2	2	.....	.....	.....	.....	.....	.....	.....	.....
	60	.....	.....	3	9	.....	.....	.....	.....	.....	.....	.....	.....
	65	.....	.....	9	16	.....	.....	.....	.....	.....	.....	.....	.....
	70	.....	.....	14	11	.....	.....	.....	.....	.....	.....	.....	.....
	75	.....	.....	10	9	.....	.....	.....	.....	.....	.....	.....	.....
	80	.....	.....	3	3	2	.....	.....	.....	.....	.....	.....	.....
	85	.....	.....	9	.....	1	1	.....	.....	.....	.....	.....	.....
	90	.....	.....	3	.....	2	.....	.....	.....	.....	.....	.....	.....
	95	.....	.....	.....	.....	2	1	.....	.....	.....	.....	.....	.....
	100	.....	.....	.....	.....	5	2	.....	.....	.....	.....	.....	.....
	105	.....	.....	.....	.....	2	5	.....	.....	.....	.....	.....	.....
	110	.....	.....	.....	.....	4	6	2	1	.....	.....	.....	.....
	115	.....	.....	.....	.....	.....	3	1	2	.....	.....	.....	.....
	120	.....	.....	.....	.....	.....	3	2	4	.....	.....	.....	.....
	125	.....	.....	.....	.....	2	.....	2	6	.....	.....	.....	.....
	130	.....	.....	.....	.....	.....	1	.....	8	.....	2	.....	.....
	135	.....	.....	.....	.....	.....	.....	.....	2	1	.....	.....	.....
	140	.....	.....	.....	.....	.....	.....	.....	1	1	3	.....	.....
	145	.....	.....	.....	.....	.....	.....	.....	1	.....	2	1	.....
	150	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	.....
	155	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	.....
	160	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1	.....
	165	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3
No.		9	10	54	50	20	22	7	26	2	9	2	3
Mean in mm.		37.8	48.3	73.1	69.0	102.3	112.3	120.1	127.4	140	146.4	156.0	165.7
Mean in inches		1.50	1.90	2.87	2.72	4.02	4.41	4.76	5.00	5.51	5.75	6.14	6.54
Standard error		.....	.....	9.1	6.4	11.9	10.3	.....	7.8	.....	.....	.....	.....

* Collected October 10, 1940.

Summary

1. Ripe males and females of *Thoburnia rhothoeca* occurred together in riffles when the water temperatures were 56° to 61° F. in early April, 1940.

2. Sexes may be distinguished on the basis of coloration of the lateral band, length of dorsal and anal fins, shape of the anal papilla, and the development and placement of pearl organs, which are better developed in the male.

3. Egg counts were 742, 1190 and 1749 in females, 108, 112, and 144 mm. in total length.

4. At the end of 1, 2, 3, 4, and 5 years they reach mean lengths of 1.9, 2.8, 4.2, 4.9, 5.7 inches total length. The largest and oldest specimen was a 6.6 inch seven year female. The longest male was 5.6 inches.

5. The sex ratio was about 1:1 until the fourth year when males are much less common. This trend continues and no males were found in the 6 and 7 year groups.

6. At two years most males mature, all spawn at three, females mature at three years.

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Reptiles and Amphibians of Smith Island, N. C.

Thomas H. Lewis

Smith Island is of peculiar interest to the biologist as a place for study of an isolated flora and fauna, and as an area of intermingling of temperate and tropical forms. It is a quadrangular land mass roughly 3.5 by 5 miles off the southern coast of North Carolina. The island emerges as a series of low hills from the inshore side of the extensive Frying Pan shoals, opposite the mouth of the Cape Fear River, and is actually composed of a group of irregular islands and tide flats strung like fingers along a broad arching beach on the seaward side. Between the fingers are salt creeks and marshes and large areas of swamp grass. The individual islands bear such local names as Baldhead, Middle Island, and Piney Island.

A number of clearly distinct edaphic areas can be described. (See Engels, 1942).[1] Behind the broad sand beach which occupies much of the periphery, is a wide zone of dunes. This in turn, breaks sharply into the forests and thickets that cover the interior, in which live oak, loblolly pine, red bay, magnolia, Bermuda mulberry, hickory, holly, wax myrtle, red cedar, dogwood, virginia creeper, wild grape, poison ivy, and smilax grow in a tangled confusion. Here the land rises to from 30 to 40 feet above the sea, the soil is rich with humus and damp with decaying logs. The forest thins in spots to open brushland, overgrown fields, and small savannas set with palmettos (*Sabal palmetto*) and cacti (*Opuntia drummondii*). These two latter plants find their most northern distribution on the island. The tropical beauty of the island is most marked in the forested zone, the heavy oaks and tall palmetto palms providing an exotic atmosphere, and the steaming shade beneath them completes the jungle picture. The physical features have been modified to a small extent by cultivation, road-building, ditching, and grazing. At present, only a few fields are being worked, and the human population seldom exceeds a half dozen persons. Semi-feral sheep and pigs are present in some numbers. The physiographic history of the island does not appear to have been studied, but certain clay-like strata seen at low tide allow the speculation that it is older than the more northern off-shore bars described in an excellent paper by Engels (1942). The accessibility in the past to the island through the more or less direct route of the shifting shoals and sand flats extending toward Federal Point is unknown, as is the length of its present isolation. It was expected, in view of the distinct contrast between the flora of the island and the adjacent coast, and of its isolation, that differences would appear between the amphibian and reptilian fauna of the island and the mainland. These expectations were not fulfilled. The interested student is referred to the works of Burt (1938) and Brimley (1939-43) for accounts of the reptiles and amphibians of the adjacent territories.

1 I have also had the privilege of examining the unpublished manuscript notes of Dr. Hugo Bloomquist on the flora of the island.

The island was visited for the purpose of collecting September 29-30, 1944 and March 28-31, 1945. Thirteen species of reptiles and amphibians were obtained. These forms apparently do not differ in any significant particular from the mainland populations, and no species were found that are not present on the immediately adjacent coast. A short list of probable forms is appended. The writer wishes to extend his thanks to Mr. Frank Sherrill, Mr. and Mrs. Gene Lewis, and to the personnel of the U. S. Coast Guard stationed on Baldhead for their hospitality and assistance in this study.

Bufo terrestris (Bonnaterre).—Large and small toads, common throughout the island, were found to be especially numerous in September.

Gastrophryne carolinensis (Holbrook).—Two narrow-mouthed toads were taken, one in the spring and one in the fall. Both were found under logs in damp forest humus.

Hyla squirella Latreille.—Three specimen in alcohol were given to me by Mr. Gene Lewis. They were in a jar with a freshly hatched specimen of Caretta caretta. No collection data. In addition three living specimens were captured in September 1944.

Rana pipiens Schreber.—A number of large green spotted frogs were seen in the field in March 1945. Tadpoles were present in enormous numbers at this time in a series of shallow sloughs. The tooth patterns of these tadpoles rule out *R. palustris*, but without adult specimens subspecific identification could not be made between *pipiens* and *sphenocephala*. On geographic grounds these frogs might safely be assigned to *sphenocephala*.

Coluber constrictor constrictor Linnaeus.—This is the most common snake on the island. It is often seen traveling rapidly through open fields, hunting in the salt marshes or dense forest, or moving slowly through the branches of low-cedars on the dunes. It is little inclined to precipitious retreats, usually standing its ground when approached or moving slowly off with head raised alertly. One was surprised with a little green snake in its mouth. Another was taken while it nosed along the margin of a slough in which frogs were common.

Elaphe quadrivittata (Holbrook).—Two specimens were taken, one at night, one at midday. Both individuals were moving through sandy areas set with scrub palmetto.

Opheodrys aestivus (Linnaeus).—Three specimens were collected. They were observed in low trees and grape vine thickets, and have been seen hunting slowly along sandy palmetto ridges.

Natrix sipedon fasciata (Linnaeus).—One aggressive specimen was captured in the sand dunes at the edge of the forest. The nearest fresh water was at least a mile distant.

Alligator mississipiensis (Daudin).—One specimen approximately six feet long was observed in a shallow fresh water slough on March 30, 1945. This individual retreated surreptitiously to a deep hole opening into a bank. The hole, roughly 30 x 10 inches, was 3 feet from the water's edge. Its depth could not be probed. Alligators are reported locally to be present in some number, but suitable terrain seems very meagre.

Anolis carolinensis (Voigt).—This is probably the most abundant lizard of the island, and can be seen in a variety of habitats; dunes, open fields, fence rows, and sandy roads of the forested interior. Several specimens, including juveniles, were collected.

Cnemidophorus sexlineatus (Linnaeus).—The three specimens in the collection were taken in September, 1944. They were found inland along the roads. All were small, 107 mm., 111 mm., and 51 mm. (broken tail).

Eumeces inexpectatus Taylor.—These skinks were found to be numerous when the island was visited in March 1945. They could be most easily captured on cool mornings by turning over boards, stones, and trash. They were seen in dry fields and also in very wet situations along sloughs. Three specimens were collected.

Caretta caretta (Linnaeus).—One small specimen in alcohol was presented by Mr. Gene Lewis. The specimen had been captured on the beach several years previously. No collecting date available.

PROBABLE FORMS

Included in this list are a doubtful sight record and forms named or described by other observers or by residents of the island. *Ophisarus ventralis* (Linnaeus), one specimen of what was probably a glass snake was unsuccessfully pursued through a pile of driftwood in September 1944. *Ophisaurus* was also well described by Mr. Gene Lewis who observed it while plowing. *Natrix erythrogaster erythrogaster* (Forster) is described by Dr. Bloomquist. One specimen of a rattlesnake (*Crotalus* sp.) is described by natives of the island as having been killed several years ago and the skin preserved as a trophy. This skin is not now available. The water moccasin, *Agkistrodon piscivorus piscivorus* (Lacépède), is described by residents also, as is the copperhead, *Agkistrodon mokasen* subsp. Soft-shelled turtles, *Amyda* sp., are reported. Mr. Keziah of Southport, N. C., says that some horned toads (*Phrynosoma* sp.) were released on the island several years ago.

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The Growth of the Slider Turtle, Pseudemys scripta elegans[1]

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Introduction

The naturalist's fragmentary knowledge of the habits and life history of turtles has been only feebly augmented since the days of Agassiz. The modern herpetologist has no thorough knowledge of the ecology of any one species and little or no information is available on the bionomics of many others.

In 1939 a long term program designed to collect data on the turtles of Illinois was initiated at Carbondale, in the southern part of the state, and data have been accumulated on many phases of the life histories of the more abundant species. In an attempt to obtain data on growth, longevity, attainment of sexual maturity, migration, home ranges, and associated problems, approximately 3000 turtles have been marked and released, and about 500 of these have been recovered at least once. Several hundred stomachs and gonads have been preserved for the study of food and for the analysis of the sex cycle.

The present report, concerning growth in the slider turtle *Pseudemys scripta elegans* Wied, represents the first segment of a long term program on the bionomics of this form. The primary purposes of this paper are: (a) to present and evaluate techniques for studying absolute growth in turtles and (b) to summarize our knowledge of the growth of the turtle named in southern Illinois.

Review of the Literature

Agassiz (1857) was the first to study the growth of turtles. On the basis of a few data on two species of *Chrysemys* and many years of observation on turtles, he suggests that the growth of turtles is exceedingly slow and that among the reptiles they are the slowest to attain sexual maturity. He concluded that females of the painted turtle do not begin to lay eggs until they are 10 to 11 years of age (1857:290). He also presents the record of a snapping turtle (*Chelydra serpentina*) that grew only one inch in 45 years.

This evidence supports the common opinion that turtles grow slowly and that they have exceptional longevity. The latter fact is further attested by Flower (1925:978), who shows that at least four species of *Testudo* have age records of 100 or more years.

The work of investigators since Agassiz show that turtles may on occasion grow rapidly. The most substantial of these studies have been made on turtles in captivity. Mitsukuri (1905:265) states that the Japanese soft shell (*Trio-*

1 A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

nyx japonicus) may reach sexual maturity in about six years. The series of reports by Coker, Barney, and Hildebrand on the culture of the diamond-back terrapin (*Malaclemys*) at Beaufort, South Carolina, indicates that the males may be sexually mature when only three and one-fifth inches in length and that females may be mature at a length of four and three-fourth inches or an age of four years. Hildebrand (1932:559) states that terrapins maintained under similar conditions may show wide differences in growth, some being nearly full grown in five or six years, while others require twelve to fifteen years or longer to reach full growth. He further states (1929:70) that after an age of 8 to 10 years it attained, growth is so slow that it is almost negligible.

Pearse (1923) made the first important analysis of growth in turtles living under natural conditions. In his report on the marking of 406 painted turtles (*Chrysemys picta bellii*) in Lake Mendota, Wisconsin, he shows that the turtles increase their length and weight 73 per cent in the second year of their life (first season of growth), 31 per cent in the third year, and 25 per cent in the fourth and fifth years. In subsequent years the rate varies from 5 to 3 per cent.

Pearse attempted to correlate growth with age, but Hubbs (1924) notes that he failed to indicate how age was determined. The records of Pearse further demonstrate much variation in growth in individuals of about the same size.

Benedetti (1925) reports that the growth rate of *Testudo graeca* varies with the size of the individual, the sex, and the seasons of the year. Townsend (1937), in summarizing his notes on the growth of Galapagos tortoises (*Testudo vicina*) retained in colonies, states that 8 individuals housed at Houston, Texas, increased an average of 137 lbs. each in 8 years and approximately doubled the carapace length.

Sergeev (1937) studied the growth of *Emys europea* and concluded that: (a) the growth is exceedingly variable, (b) the growth is rapid in juveniles but ceases completely in old individuals, and (c) the attainment of sexual maturity does not result in a slowing of growth. Liu and Hu (1940) conclude that the growth of *Geoclemys reevesii* is rather rapid and constant during the first five years but irregular and slow afterwards. They suggest that this slowing of growth may be due to the attainment of sexual maturity.

Parker (1929:371), in summarizing his discussion of growth in turtles, states, "It is clear from the evidence presented in this paper, that turtles, even large ones, may reach maturity at a comparatively rapid rate, and that the opinion commonly entertained of their great slowness of growth is scarcely justifiable. Without doubt their increase in late life is very slow and this may have given occasion for the belief in a low rate of growth in general. Such rates, however, do not apply to their early states."

The above citations represent the principal studies of turtle growth. There are many scattered observations in the literature of vertebrate zoology.

These past researches indicate, in general, that growth is much more rapid in juveniles than in mature individuals; that there is much individual variation in growth; and that turtles are rather long-lived vertebrates.

Methods

The ideal method of studying the growth rate of any animal is to make repeated observations at regular intervals on the same individuals living under the same natural conditions. Unfortunately, it is rarely possible to do this. The next best plan is to measure a large number of individuals and to study each one whenever and wherever it may be available. This procedure requires access to a rather large population, a dependable marking system, and an accurate method of measurement. Turtles have been collected and marked according to the latter plan since 1939 (Cagle, 1942:1944a).

Since I was interested in: (a) relative and absolute growth of the carapace and plastron, (b) secondary expressions of sexual maturity, (c) size and age groups, (d) possible value of the use of growth rings in growth analysis, and (e) determining which of the measurable structures were most reliable as growth indicators, the following set of measurements was selected:

Carapace length	Maximum length of carapace
Carapace width	Maximum width of carapace
Plastron length	Maximum length
Plastron width	Maximum width of posterior lobe
Height	Maximum height
Preanal region	Length from posterior edge of plastron to anterior lip of anus
Postanal region	Length from posterior lip of anus to tip of tail
Third claw	Length of third claw taken in straight line from base to tip
Plastral annuli	The maximum length of each annulus on the plastral plates. (pl. 2)

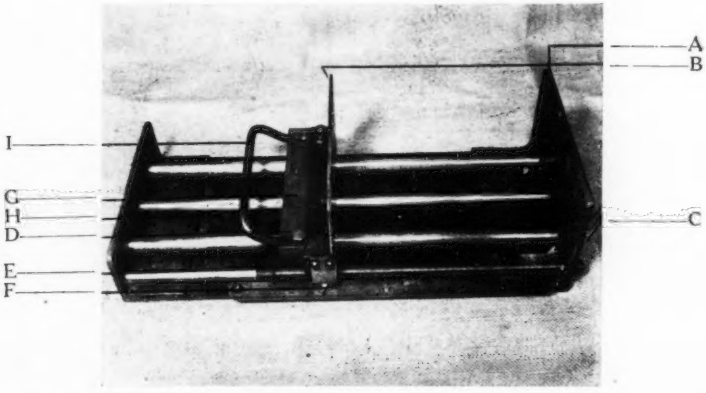


PLATE 1.—The measuring device. A turtle was measured by placing it against the fixed plate (a) and moving the sliding plate (b) until it was in contact with the turtle. The marks (c) indicate the points at which the carapace or plastron should come in contact with the plates. Once the sliding plate was in position the steel spring (d) was depressed and the measurement read from the rule (e) as indicated by the pointer (f). The movable plate is attached to a heavy steel bar (g) sliding on steel rods (h) which penetrate it. The handle (i) makes it possible for the operator to more adequately control the pressure with which the plate is pushed against the turtle.

After much experimentation a steel measuring instrument was devised (pl. 1). This instrument consists of a heavy ¼ inch steel base on which are mounted 3 steel rods each ½ inch in diameter. A vertical plate at one end serves as the fixed point in the device. Opposite this there is a sliding plate mounted on a 1½ square steel bar pierced by the rods. The holes in the bar and the rods were fitted so closely that an oil film had to be maintained on the rods to allow movement. An adjustable metal pointer affixed to the steel bar moved above a standard metal rule marked in millimeters. A rod cut with millimeter threads was fixed to the base and the pointer was attached to a piece of spring steel permitting the pointer to deviate slightly to either side. A short section of rod cut with millimeter threads was fastened to the underside of the spring so that when the pointer was depressed the threads engaged the rod mounted on the base and thus moved the pointer to either the right or left, automatically indicating the nearest millimeter. A turtle to be measured was held at the proper point[2] against the fixed plate and the movable one pushed gently forward until contact was made. The measurement was read from the metal rule to the nearest millimeter. Marks on both vertical plates indicated the points for placing the carapace and plastron for measurement.

Young turtles on account of the flexible carapace and plastron, were measured with a more delicate instrument, the vernier caliper. This was also used in making the preanal, postanal, and third claw measurements.

Although weights were taken of many individuals, they were not regarded as of great significance because of the great weight of water irregularly carried by the turtle and the weight of the feces, which in some instances amounted to one-tenth the total weight of the turtle.

The growth rings of the plastron provided a second source of data for growth analysis. In a growing individual, these are formed at intervals on each of the plastral plates and provide a means of determining a portion or all of the growth history of an individual.

PROCEDURES IN RELEASE AND RECOVERY

All turtles were removed to the laboratory within a few hours after capture, where they were measured, marked, and photographed in color. Those not detained for stomach or gonad studies were then returned to the lake or stream from which they were removed.

THE AREAS STUDIED

These investigations were conducted in two principal areas, the Carbondale City Lake with its associated ponds and a segment of the drainage ditch system of the Mississippi flood plain. Population samples for comparative studies have been taken from many other lakes, ponds, and streams of southern Illinois.

City Lake is about three-fourths of a mile long and one-half mile wide with a maximum depth of 25 feet, average depth approximately 5 feet. As a

2 A serious amount of error is introduced if extreme care is not taken to make all measurements in identical planes.

result of activities of the city water company, there is little aquatic vegetation and much of the shore line has been stripped of plant growth, thus eliminating much of the invertebrate life. The game fish are few and the lake is dominated by large, rough fish. Few basking sites and few favorable feeding areas are available for turtles.

Immediately adjacent to City Lake there are 3 small, artificial ponds. Thomas Pond is a small, clear-water pond, approximately one acre in extent, with a rich fauna and flora. The other two are typical, small stock ponds with clay shores and bottoms.

Within a radius of one mile of City Lake there are 3 other permanent water bodies. The largest of these is Thompson Lake, an artificial lake rich in plants and animals. Lake Ridgeway is a small pond on the college campus. To the south of Lake Ridgeway is the state pond located on the property of the state farm. Piles Fork Creek, a small stream running near the state pond and thence to the overflow of City Lake, is dry throughout much of the year but does provide a highway for turtles moving between these water bodies and City Lake (Cagle, 1944b).

The second general region, a segment of the drainage ditch system of the Mississippi flood plain, consists of a main ditch approximately 7 miles long and 2 principal tributaries each about 4 miles long. These ditches, constructed to drain the swamps of the region, are 15-30 feet deep and 20-50 feet wide at the top. During seasons of normal rainfall the main channel and lower reaches of the tributaries contain several feet of water and support a lush growth of aquatic vegetation and a large population of vertebrates, most of which move into the ditches from the river sloughs. During drought seasons these ditches dry up, forcing the aquatic life to aestivate or move long distances down the dry channel to the river (Cagle, 1944b).

The Annual Activity Cycle

The interpretation of the growth records depends on a knowledge of the annual activity cycle. It was essential to determine the limits of the growing season—when *Pseudemys* becomes active in the spring, takes its first food, shows the first evidence of new growth, and becomes quiescent in the fall. The necessary answers to some of these questions were obtained by sample trapping; by field observation of feeding, courtship, and basking; by examination of gonads and stomachs; by analysis of growth ring and recovery records; and from temperature records and experiments.

The temperature records promised to yield the most satisfactory means of defining the growing season. Unfortunately, scant information is available on the minimum and maximum temperatures at which turtles become or remain active. Baldwin (1925:443) found that neither the snapping turtle (*Chelydra serpentina*) nor the painted turtle (*Chrysemys picta*) could withstand a body temperature of 102°-105° F. (39-41° C.) for as long as thirty minutes and that individuals of both species become relatively inactive at temperatures below 50° F. (10° C.). Hildebrand and Hatsel (1927:376) report that 2 of 3 loggerhead turtles confined in an enclosure were frozen to death when the air temperature dropped to 26° F. (-3.3° C.), the third surviving down to

13° F. (−10.6° C.). Casual observations have been made by others on turtles moving about in ice-covered lakes, thus evidently at temperatures between 0° and 4° C.

Some work was undertaken to secure data basic to determining extremes of environmental temperature limiting the normal activities (maximum and minimum effective temperature) on the assumption that little or no growth occurs beyond the extremes. Field records were made of air and water temperatures at the time turtles were observed with subsequent study of the correlation of basking, feeding, and courtship with temperature; the rate and extent of temperature increase in basking turtles were studied and laboratory observations of turtle activity were made for various water temperatures.

No thermocouple or thermostat was available and the improvised procedures were accurate only to about 1° C. The temperature of individual turtles was taken by inserting a thermometer one-half to 2 inches into the cloaca for 3 minutes. Water and air temperatures were taken with the same thermometer.

In one experiment a juvenile female, 110 mm. in plastron length, was placed in a container of water in a refrigerator unit. At 8:45 A.M. when the turtle was placed in the water its cloacal temperature was 21.3° C., the water temperature 13° C. The turtle was quite active and moved rapidly about in the container when disturbed. One hour later the water temperature was 7.8° C., the cloacal temperature 19.3° C. When disturbed, the turtle executed slow swimming movements. Two hours later the water temperature was 3.4° C., the cloacal temperature 5.7° C. and the turtle reacted only feebly to external stimulation. It did not attempt swimming movements but merely tried to retract its head and feet into its shell. After 9 hours the turtle was found with the feet and tail frozen in one-quarter inch of ice. It did not react to any stimulus applied and was assumed to be dead; but when placed in cool water, it recovered without any apparent ill effects.

This crude experiment suggests that the minimum effective temperature for the species is about 10° C. as at this point swimming movements were so slow as to be ineffective. It supports the popular belief in the ability of turtles to withstand freezing temperature for a short time.

The basking experiments were performed to gain information on the absolute maximum body temperature. It should be pointed out here that under normal conditions the turtle experiences the minimum effective temperature in the water habitat and the maximum while exposed to the direct rays of the sun.

In a preliminary experiment a large female was placed in bright sunlight with the plastron turned upward. Although not the normal basking position, it discouraged the turtle from making attempts to move about and made cloacal insertion of the thermometer simpler. Cloacal readings taken at irregular intervals showed an increase from 17° to 37.2° C. in 180 minutes (Fig. 1). When the cloacal temperature reached 34° C, the turtle was quite active and made strong attempts to escape. It continued those endeavors until its temperature reached 37.2° C., when all movements became convulsive and the turtle was removed to a cool place, where it recovered.

That turtles can survive such high temperatures is indicated by one field experience. In June, 1941 a drainage ditch south of Dixon Springs, Illinois, was checked for turtles. The water was very low and was distributed in scat-

tered pools a few inches to a foot deep. In one of the shallow, gravel bottomed pools in which the water temperature was 37° C., the turtles were very active. Those that could ordinarily be handled carelessly with impunity, snapped and scratched viciously when caught. Three species, *Chrysemys picta* ssp., *Pseudemys scripta elegans* and *Kinosternon subrubrum* ssp., were taken from this pool.

In a second experiment, 5 turtles that had been out of water for several hours were placed in the sun and cloacal temperatures taken at 5 minute intervals. The air temperature was 18.8° C., and cloacal temperatures ranged from 13.9° C. to 15° C. All were quite sluggish to begin with but their response to the insertion of the thermometer became more pronounced as the temperature increased. When 18° C. was reached the turtles appeared to be normally active. The cloacal temperatures increased 12.4° to 14.9° C., mean increase 13.5° C., in 168 minutes, i.e., to 28.8 to 30° C. None of the turtles showed any evidence of discomfort (fig. 1).

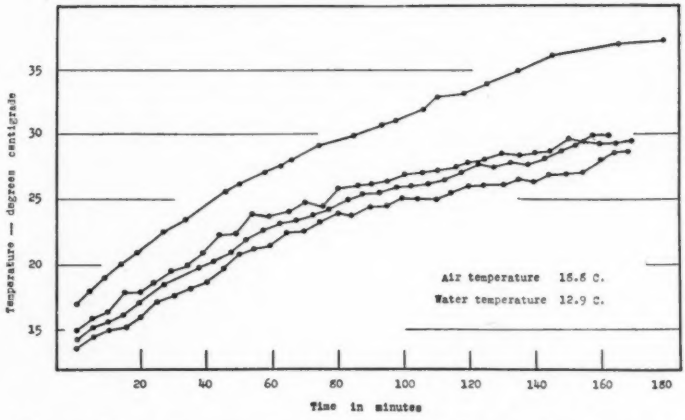


Fig. 1.—The rate of temperature increase in four turtles exposed to direct sunlight.

These experiments suggest that the maximum effective temperature is about 37° C., that the optimum temperature is between 18° C. and 30° C., that the temperature of a basking turtle may increase rapidly, and that the length of a basking period is determined by the water and air temperature and the intensity of the sun's rays. These experiments are crude but it appears logical to infer that the period of normal activity in nature is limited within the internal temperature range of approximately 10° to 37° C. The turtles doubtless do not feed beyond the extremes of this temperature range and consequently do not grow.

Since it has been demonstrated (Baldwin 1925:432) that the difference between internal temperature and environmental temperature fluctuates only from 1.5° C. to 3° C. within the non-critical range, I deduce that spring activ-

ity begins when the temperature reaches approximately 10° C. and that fall quiescence is initiated when the water temperature returns to the same level.

Field studies formed the most satisfactory basis for an outline of the activity cycle. Traps of two types, box traps and 3 hoop, single-throat nets were run at irregular periods in City Lake over a three year period and records of the number of turtles caught per hour in each set recorded (Fig. 2). Turtles were collected in each month except December, January and February. The trapping records indicate that the peaks of acitvity are reached in May and September with a decline during June and July. The activity peaks correspond with mean monthly water temperatures of 21.7° C. (71° F.) and 25° C. (77° F.) and the decline in activity with high water temperatures. Other observations substantiate these conclusions.

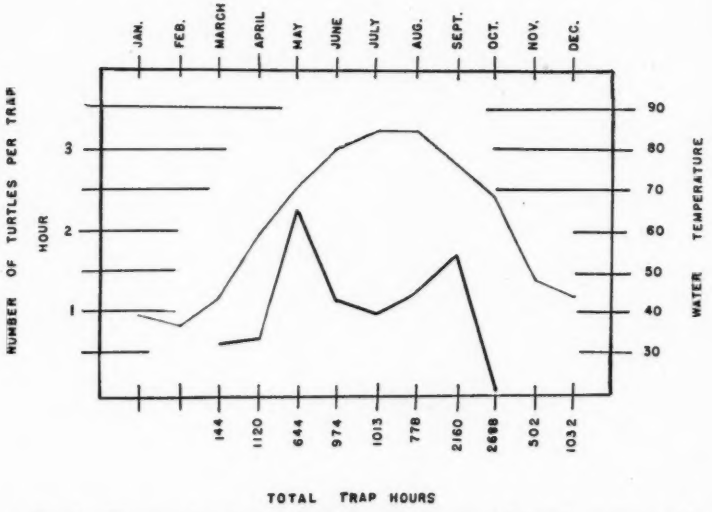


Fig. 2.—The annual cycle of activity. The upper curve indicates the mean monthly temperatures during 1940; the lower curve, the number of turtles per trap hour in each month.

No *Pseudemys* was observed in January although the lake shore was scouted many times and traps were set on several occasions. That all species of turtles were not inactive at this time is shown by the fact that 9 examples of *Chrysemys* were collected from a mine pond in January, 1938, where the water temperature was 11.1° C.[3]

Three live turtles were found on the shore during the warmer days and 14 juvenile turtles were collected from shallow water in February. None of the

3 Conant (1938:149) states that painted turtles (*Chrysemys*) were collected during every month of the year in the Toledo Ohio area and were frequently observed moving about under the ice.

turtles collected in the water were moving about and those basking made no attempt to retreat to the water. One of the 14 juveniles was seen through ½ inch of ice and was so sluggish it did not escape while the collector broke the ice to reach it. All of the stomachs were empty.

One of the basking turtles collected from the shore made no movement when picked up. The limbs were completely relaxed and the anus remained open after the thermometer used in taking the cloacal temperature (13° C.) had been removed. Another turtle collected from a similar situation made no move to escape; it simply pulled in its head and legs when touched. Its cloacal temperature was 12.8° C.

On the warm days of late March when the air temperature rises above that of the water, occasional turtles may be observed but no mass basking occurs. Turtles are easily collected from shallow water during March; the water is still not warm enough to allow more than feeble movements but the turtles appear to be restless and wander slowly about the bottoms. Turtles were frequently collected on shore or from basking sites where they had apparently dallied so long that they had become too numb to return to the water. None of those collected in March contained food in their stomachs although crayfish, tadpoles, and dead fish were observed along the shore in relative abundance.

Throughout April there is an increase in activity. Numbers of turtles may be seen at the basking sites and the first evidences of spring courtship behavior may be noted. On April 20, 1940, 163 basking turtles were counted within 100 feet of an observation tower and courtship was repeatedly observed.

May, June and July field data indicate that the turtles are in the height of the courtship activity during May. Feeding activities were observed during these months and basking turtles were numerous on every warm day.

During late August and early September courtship behavior again was the most prominent activity observed. Many of the ponds, lakes, and streams reach low levels in September; the water becomes quite warm and many individuals move overland long distances from one body of water to another (Cagle, 1944b).

In October one notes a slackening in the activity of the turtle. Observations indicate that water temperatures are so lowered that most turtles seek hibernating quarters or simply settle to the bottom in shallow water where they probably remain until warmed by the spring sun.

A large number of turtles was collected in a cypress slough near Cypress, Illinois, in October, 1939. The turtles had burrowed into mud and debris at the edges of shallow pools in the swamp or had crawled into the hollow decaying cypress stumps, where some were literally stacked in layers. All were quite sluggish and all of 40 stomachs examined were empty. The water temperature was 10° C. on October 22, 1938, when 42 turtles were taken from a cypress stump from which 10 had been taken on a previous day.

During November turtles show little activity. A few individuals were collected from the mud flats at City Lake and on some days turtles were observed basking. Field observations in November 1939, indicate no activity when the water temperature was 10° C. or less but at 3 different times when water

temperatures were 12.8°, 12.8° and 15° C., turtles were moving about in the water and some were basking. On November 25, 1938 one large male of *Pseudemys* was observed moving feebly under the ice on a small pond. The water temperature was 2.7° C.

Turtles collected during December from the mud flats of City Lake were inactive and their stomachs contained no food. Turtles were observed basking on logs in December.

These field observations indicate that the turtles cease feeding in October and are active only as the water temperatures permit during the winter months. The first considerable amount of basking occurs in March, but there are no great numbers of individuals at basking sites until the last of April and the first of May. There is no appreciable basking activity when the water temperature is less than 10° C., but when the water had reached 12° to 15° C., three turtles were observed moving about in the water and basking. It is probable that the minimum effective temperature for *Pseudemys* and perhaps other turtles as well is approximately 10° C.

On this assumption turtles would begin their activities about the middle of March and end them during the latter part of October. This is verified by the fact that the first trapping returns were obtained in March and the last in October. The activity curve for *Pseudemys* based on the number of turtles collected per trap hour corresponds well with one prepared by Conant (1938) on the basis of the number of specimens brought to the Toledo Zoological Park in each month. His records show that turtles are comparatively inactive from October to March, a total of only 33 being collected in that period as contrasted with a total of 354 in the other months. From March there was a monthly increase in the number of turtles reported to a maximum in June with a subsequent decline. Conant's graph indicates that the first large collections were made in April when the mean monthly temperature was approximately 48° F. (8.89° C.) and the largest number was reported in June when the temperature was approximately 72° F. (22.2° C.). In October, when there was a decided reduction in the number of turtles collected, the temperature was approximately 53° F. (11.7° C.).

The optimum environmental temperature for *Pseudemys*, from examination of the activity curve, appears to be about 21° C. (70° F.), as both peaks occur at that water temperature (Fig. 2).

The period of egg laying falls within the first activity period. Thirty females containing eggs ready to be laid were collected in May, June, and July during the four years of study. Females were seen depositing eggs during May and June, and many nests were found in early May.

From all of my observations the growing season must fall essentially within the period from late April to early October.

Other workers have similarly defined the period of activity for other species. Hildebrand (1932:553) reported that the annual active feeding period of terrapins is comparatively short. The animals are seldom continuously active and feeding regularly before the first of May and by the middle of October they become inactive and cease feeding. He states, "The animals are so sensitive to temperature that even during cool days in mid-summer their capacity for food consumption is markedly reduced."

Butler (1885:37) notes that the box turtle enters the ground in southern Indiana during the latter part of September or early in October. Penn and Pottharst (1940:27) state that the box turtle (*Terrapene carolina*) entered hibernation when the temperature dropped to near 65° F. (18.3° C.). Conant reports that of 182 spotted turtles (*Clemmys guttata*) 12% were found in March, 28% in April, and 40% in May. Risley (1933:690) states that the earliest collections of musk turtles (*Sternotherus odoratus*) were made in late March. Everman and Clark (1920:607) state that the map turtle (*Graptemys geographica*) does not hibernate but is active all winter and may be observed through the ice walking about on the bottom. Abbott (1884:37) who observed 9 species of turtles concluded that there is considerable winter activity, even when they are not feeding.

These reports of winter activity indicate, as would be expected from the lag in temperature change of water, that the terrestrial turtles begin hibernation earlier than aquatic ones in the same area. My own observations indicate that turtles may move about at air temperatures as low as 15° C. It also appears that the minimum effective temperature is not the same for all species. Cahn

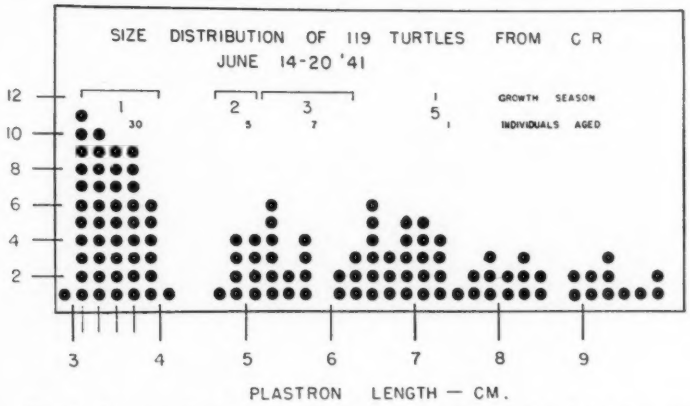
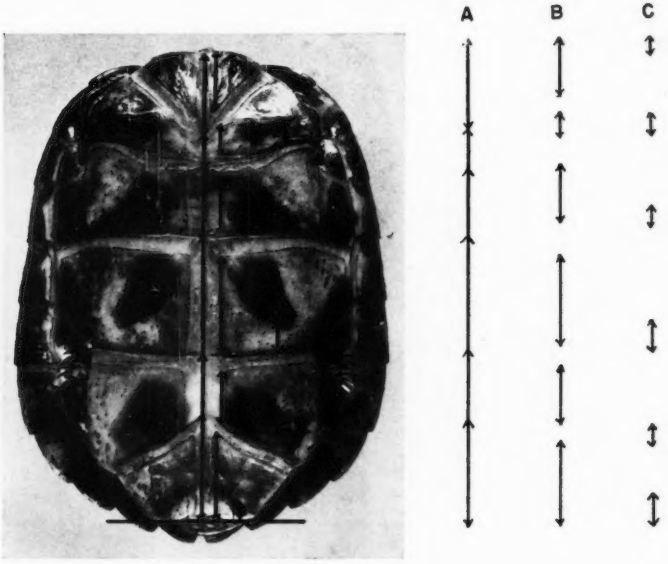


Fig. 3.—The size distribution of 119 turtles collected from City Lake, June 14-20, 1941.

(1937:102) observes that *Terrapene ornata* enters hibernation about 2 weeks earlier and remains there nearly a month longer than *Terrapene carolina*. He further reports that *Chrysemys*, *Chelydra*, and *Terrapene* enter hibernation in sluggishly active through the winter in southern Illinois and enters hibernation during October in the northern part of the state.

The growth records of turtles released and recovered offer a more accurate definition of the growing season. The majority (87 out of 104) of the turtles in the size range 20-100 mm. released for any substantial part of the period from May 1 to October 1 shows some growth, but none of those at liberty October and emerge about mid-April; but he suggests that *Graptemys* remains only during the period of October 1 to May 1 grew at all.

Some of the turtles recovered after being released for comparatively short periods during the growing season had grown rapidly. This was particularly true of turtles in the 20-50 mm. group. No. 2337, released for 62 days, increased 7 mm. in plastron length. No. 2512, released for 78 days, grew 10 mm.; No. 2513 grew 7 mm. in 26 days; No. 2514 grew 16 mm. in 78 days; No. 2627 grew 14 mm. in 55 days. Turtles released within the period October 1 to May 1 and those released for part of the growing season and the winter season exhibited much less growth. Two individuals at liberty during two winters and the growing season of 1940 grew approximately the same



Σ A—Present plastron length.
Σ B—Plastron length at first of growing season.
Σ C—Plastron length at first of previous growing season.

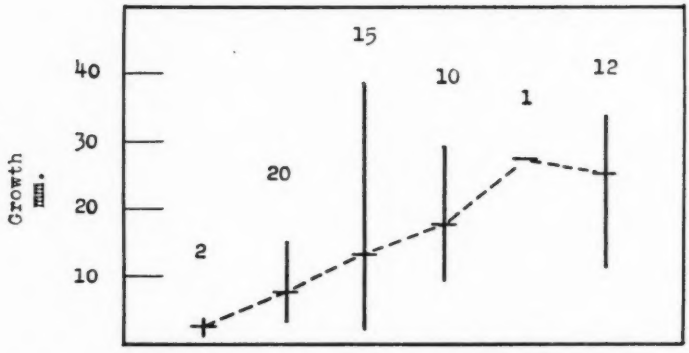
PLATE 2.—The method of measuring growth rings. The length of each ring is measured between the points indicated by the black arrows, and the sum of the lengths of the rings in each set used as the plastron length at a time determined by the date of collection and the condition of the growth zones.

For example, this individual, collected June 12, 1941, has two distinct sets of growth rings, the smaller of which (c) indicates the size of the birth plates. Since the turtle was collected near the middle of its growing season and the last-formed growth zone is conspicuously lighter than the other, we may conclude that the last zone represents growth made during the season of 1941. Further, in view of the presence of birth plates we may conclude that the turtle is in its second season of growth.

The amount of increase in plastron length for this first season may be obtained by subtracting the sum of (c) from the sum of (b); the growth for the second season (43 days in the season of 1941), the sum of (a) minus the sum of (b).

amount as four released only in the 1941 growing season; in other words, growth was limited to the growing season.

Growth zone measurements (pl. 2) also indicate that the first growth of the season occurs in May, and that growth is continuous to October. Turtles collected in May were the first to show distinct growth zones forming (fig. 4). The mean growth for each month shows a steady increase to October, when, with the exception of a single September record, the peak is reached. Variation is to be expected in the length of the growing season as a result of fluctuation in such factors as temperature, food, and water level. Juvenile turtles collected in mid-growing season frequently showed no growth. Of 129 turtles collected from the mudflat at City Lake, June 14-20, 1941, 86 had not grown so far that season, 25 had grown slightly, and 18 exhibited conspicuous growth.



	May	June	July	Aug.	Sept.	Oct.
Maximum	4.0	13.8	38.1	29.5		33.9
Minimum	2.3	3.3	2.1	9.3		11.4
Mean	3.1	7.1	13.4	17.7	27.6	25.4

Fig. 4.—The monthly growth increment of turtles in their first season of growth at City Lake.

Hildebrand (1929:45) states that young terrapins "do not feed regularly until about the latter part of May and do not make perceptible growth for a month or more after regular feeding takes place."

These combined observations indicate that growth begins in May and ends in October; arbitrarily, as a matter of convenience, this period will be hereinafter considered as extending from May 1 to October 1.

Use of Plastral Annuli in Growth Studies

The borders of the scutes of most turtles are margined by grooves that have commonly been called growth rings. Since the term "annuli" has been widely accepted for the similarly formed rings in fish scales, it will be convenient to use it here; I have used "growth ring" and "ring" as alternates. The

study of these annuli in *Pseudemys* promised a method of determining age and a supplementary method of studying growth. It soon became apparent that the accumulation of growth data through the study of marked turtles would be slow and cumbersome and some additional means of growth study was sought.

The annuli are slight indentions in the horny plates, impressed also on the underlying bone. The shape of the groove varies considerably in individual turtles and in successive years. In some instances it is steep-sided and deep and in others wide and shallow, probably a reflection of growth conditions. The annuli bound each plate of the carapace and plastron. In some species that do not shed their horny plates, they remain visible until they are worn off. In those that do shed, the rings fade with each successive shedding and there are rarely as many as five rings visible.

Investigation on other species of turtles throws light on the value of the annuli for age determination. Ewing (1939:90) indicates that in *Terrapene carolina* they are produced by the slower and more irregular formation of the horny substance during the period of hibernation. Townsend (1937:290) points out that the tortoises (*Testudo vicina*) housed in the winter developed a conspicuous white growth zone when turned out on grass in the spring. He states, "This treatment produced a new ring each year, indicating age; growth slow in winter, rapid in summer. Tortoises in southern Florida, having access to grassy ranges at all times, were never lacking a faint whitish ring. However, tortoises of similar size and weight had equal numbers of rings, regardless of treatment." He further indicates that the rings are valid growth indicators in the younger animals but that it is difficult to count rings in the older ones.

Nichols (1939:16), referring to *Terrapene carolina,* shows that the first 5 or 6 annuli are probably added regularly, one each year, and later on years are missed with increasing frequency. He found that in 5 turtles the number of annuli added corresponded exactly with the number of years released. One turtle added only one in 8 years; another only 2 in 7 years. It is of importance to note that all turtles adding few annuli as compared with the number of years released were more than 6 years old and 2 were more than 13. Three individuals added one more annulus than the number of years released.

Miller (1932:195) studied the changes in the third vertebral scute of a number of desert tortoises (*Gopherus agassizii*) kept in captivity. He found that the annuli formed at the margin of the hatchling scutes retained their original dimensions even though the turtle had doubled in size, but that study of known two-year-olds and of larger animals of unknown age proved that formation of annuli may be irregular. He points out that this is what might be expected in the desert where growth conditions fluctuate; but under animal house conditions, where the food supply is continuous and temperature the dominant influence, the annuli are still irregular and do not accurately reflect seasonal activity.

Hildebrand and Hatsel (1926:13) find that the annuli are reliable age indicators in the younger diamond-back terrapins, but not in mature specimens, and Risley (1933:703) comes to the same conclusion for the musk

turtle. Benedetti (1925) in a study of *Testudo graeca* could determine the age of only 94 of 340 individuals through the use of annuli.

Obviously the value of the annuli as age indicators varies not only with the species but also with the habitat occupied by the individuals in question. Any interruption in the supply of food or ability of the individual to utilize food might result in the cessation of growth and the formation of an extra annulus or in none being formed for a given season. A turtle might remain in a pond for several weeks after it has become completely barren of food and then move to another area where food is abundant, and this might result in the formation of an annulus. There is ample evidence to indicate that some individuals may not grow for several seasons and may not form annuli.

Pseudemys presumably is subject to the same sources of irregularity of its annuli are are other turtles. An occasional specimen exhibits a weakly defined annulus that might well represent a temporary cessation or slowing of growth during the growing season.

The first annulus is formed in *Pseudemys* of southern Illinois by the cessation of growth during the first winter of life and the subsequent rapid growth during the first season. Since during the progress of the growth research no hatchling turtles were observed to grow during the interval between hatching and the beginning of the first period of winter quiescence, it is apparent that the first annulus marks the boundaries of the birth plates.

As long as this ring is visible one may reasonably assume that all the annuli ever formed are present but once it is lost the assumption can no longer be safely made. This first annulus in *Pseudemys* is rarely visible after 3 years; of 56 turtles retaining it only one had more than 4 annuli.

However, the annuli would be of much importance in growth studies if it could be demonstrated that: (a) in most individuals not more than one is formed annually, (b) the zone between any 2 annuli represents one season of growth, (c) the approximate period of time represented by any area between rings is determinable.

The only satisfactory method of checking points (a) and (b) was to compare annuli on individuals at the time of release and the time of recovery.

During 3 years the measurements of the annuli on the plastral plates of 28 *Pseudemys* were taken at both the time of release and the time of recovery (Plate 2 and table 1). These data indicate that the annuli are formed annually and that the area between any 2 annuli represents one season of growth. For example: No. 215, when collected July 27, 1939, had 3 sets of annuli visible, the largest of which totaled 113 mm. in length, theoretically the plastron length at the end of the 1939 growing season. This turtle was again taken on September 17, 1940—approximately 14 months after its release. If annuli are formed during the period of hibernation, this turtle would be expected to have added one set during the interval of release. When the plastron was examined only two annuli were found; the smaller, measuring 112 mm., was undoubtedly the same set that was present in 1939; the larger, measuring 123 mm., was the one formed during the winter of 1939-40. Two annuli had been lost. Evidently the annuli fade rapidly. All the other turtles growing during the release period formed one annulus for each winter period released (table 1).

TABLE 1.—The comparison of annuli at time of release and recovery.

No.	Date collected	Sum of lengths of annuli (plastron length at the end of the season indicated)					
		1936	1937	1938	1939	1940	1941
215	7/27/39	99.2	108.3	113.0	.....	.....	.....
	9/17/40	.....	.....	112.0	122.8	.....	.....
217	7/27/39	.....	89.5	100.7	.....	.....	.....
	8/21/39	.....	.....	101.2	.....	.....	.....
232	7/27/39	31.2	41.4	54.5	.....	.....	.....
	9/1/42	.....	.....	.....	.....	.....	80.4
236	7/28/39	.....	.....	96.1	.....	.....	.....
	5/3/41	.....	.....	.....	107.3	.....	.....
244	7/30/39	.....	.....	111.4	.....	.....	.....
	4/25/41	.....	.....	.....	.....	126.5	.....
246	7/31/39	.....	.....	137.7	.....	.....	.....
	8/6/41	.....	.....	.....	.....	143.5	.....
269	8/9/39	.....	97.0	107.0	.....	.....	.....
	8/11/41	.....	.....	.....	110.9	119.8	.....
273	8/9/39	.....	52.2	64.5	.....	.....	.....
	5/3/41	.....	.....	.....	75.3	84.4	.....
275	8/9/39	72.8	80.7	91.1	.....	.....	.....
	9/11/42	.....	.....	.....	.....	87.8	98.6
289	8/11/39	.....	99.7	112.2	.....	.....	.....
	8/14/41	.....	.....	.....	.....	134.2	.....
297	8/11/39	99.6	113.3	126.6	.....	.....	.....
	4/23/41	.....	.....	128.3	138.9	150.7	.....
299	8/11/39	.....	.....	145.0	.....	.....	.....
	8/5/40	.....	.....	.....	150.7	.....	.....
301	8/11/39	110.7	121.3	126.2	.....	.....	.....
	8/6/41	.....	.....	.....	132.5	148.1	.....
315	8/11/39	.....	106.6	119.5	.....	.....	.....
	8/1/41	.....	.....	.....	128.7	137.1	.....
318	8/11/39	.....	101.0	113.1	.....	.....	.....
	5/6/41	.....	.....	.....	125.0	132.1	.....
356	8/26/39	.....	76.1	83.6	.....	.....	.....
	8/18/40	.....	.....	.....	92.6	.....	.....
369	8/26/39	.....	93.6	105.6	.....	.....	.....
	5/18/40	.....	.....	.....	107.7	.....	.....
497	5/19/40	.....	99.3	116.6	.....	.....	.....
	4/25/41	.....	99.6	113.8	131.0	135.2	.....
544	5/18/40	.....	81.9	90.8	.....	.....	.....
	5/5/41	.....	.....	.....	94.5	99.6	.....
638	6/30/40	.....	.....	.....	30.0	.....	.....
	5/23/41	.....	.....	.....	31.9	50.5	.....
664	7/2/40	.....	.....	84.8	97.1	.....	.....
	5/3/41	.....	.....	.....	99.0	108.7	.....
665	7/2/40	.....	.....	97.5	112.2	.....	.....
	5/1/41	.....	.....	99.2	113.4	.....	.....
691	7/10/40	.....	.....	.....	30.5	.....	.....
	5/23/41	.....	.....	.....	.....	45.1	.....
719	7/27/40	.....	.....	87.4	100.4	.....	.....
	8/6/41	.....	.....	.....	.....	114.5	.....
728	8/3/40	.....	.....	65.7	78.7	.....	.....
	5/22/41	.....	.....	.....	83.8	90.5	.....
813	9/18/40	.....	.....	.....	94.0	.....	.....
	8/6/41	.....	.....	.....	.....	98.9	.....

See page 727 for key to abbreviations used in the above table.

A turtle that hibernates without having grown during the growing season can form no additional annulus. When growth is very slight, the annuli are close together and may even blend on some portions of the scute.

The area between two successive annuli, which may be designated as the growth zone, represents the growth for one season. The period represented by a particular growth may be determined by the date of examination and the appearance of the growth zone. In a turtle collected in July, the middle of the growing season, if the growth zone is light in color and covered with only a thin layer of horn, it may be concluded that the zone represents that season's growth. If the growth zone is well pigmented and covered with thick horn, it presumably did not represent growth during the season collected, but that of a previous season. New growth is easily detected and would only rarely be confused with growth made during an earlier period.

It remains to test the assumption that increase in the size of the plastral plates is by simple additive growth.

The simplest demonstration of this is the fact that annuli remain the same size once they are formed. Thus the annuli that form about the margins of the birth plates remain distinct in many turtles for several years and may easily be measured. Measurements made of the first formed annuli of 144 individuals varying in age from one to 5 seasons ranged from 23.1 to 35.0 mm., mean $30.8 \pm .18$ mm. For comparison, and also as further test of the validity of the annulus measurement method, the plastral lengths of 65 hatchlings 24 to 48 hours old were measured. The range of this measurement was 24.5-33.0 mm., and the mean, $29.8 \pm .24$ mm. Since the standard error is contained in the difference between the means only 1.6 times we may conclude that the first formed annuli had not increased significantly in length. This type of growth is further demonstrated through the close correlation of measurements taken of the same sets of annuli at intervals (table 1).

Although annuli once formed do not change in size, the repeated shedding of the scutes does cause them to disappear so that the number visible depends on amount of growth and the age of the turtle.

For determining growth from measurements of annuli, the sum of the lengths of the annuli (one on each plastral plate) is used as the plastral length of the individual at the time the annulus was formed, and the sum of the lengths of the plastral plates as the present plastral length. The difference between the two sums then represent the actual increase in length of the plastron during the period represented by the growth zone (pl. 2).

Sergeev (1937) has used the method, suggested by Lea for the determination of growth in fishes from study of scale dimensions, a technique now in extensive use by ichthyologists. Sergeev used the formula $\frac{L_1}{L_2} = \frac{C_1}{C_2}$, where L_1 was the unknown, L_2 the length of the turtle, C_1 the length of the annulus, and C_2 the length of the scute in question. He used, experimentally, the annuli on various plates of the plastron and carapace of several species (*Testudo ibera, Emys europea, Chrysemys concinna*) and compared the results obtained by this procedure with the results obtained by the study of the sizes of turtles

of known age. He concluded that this method could be utilized in the analysis of growth of all those turtles that form annual rings.

This technique, a rapid and efficient method of making growth determinations, is in use in the growth research in Illinois. To date, the annuli of the pectoral plate only have been used and results have been satisfactory. Since it is apparent that there are some relative growth changes in the plastron plates, it is suggested that before the technique be used in growth studies the validity of the use of the plate selected be demonstrated in the species concerned (i.e., that the length of the plate retains a constant relation to the length of the plastron throughout the life of the individual).

The method as employed by Sergeev was used experimentally with *Pseudemys*. In 28 individuals it has been possible to compare the growth as determined by three methods: release-recovery, measurement of all plastral annuli, and computation from the measurements of pectoral scute annuli (table 2). In most of the individuals studied results from the three methods agree. No. 150, when released for 257 days in the growing season, grew 21 mm. Its growth as calculated for 306 days of the growing season on the basis of annulus measurements was also 21 mm. With few exceptions (see nos. 2396, 2412) the remaining records demonstrate the validity of the use of annulus measurements in computing growth.

In computing growth from annulus measurements, the length of the plastron must be considered as the sum of the lengths of the plastral plates and not as the overall length of the plastron. If the total length of the plastron is measured in one step and used in computing the growth, error will result, because of the slight curvature of the plastron.

The annulus measurement procedure may be used in conjunction with the release-recovery method to delimit the period in which growth occurred. Individual No. 236 (table 2), released July 28, 1939, and recovered May 3, 1941, increased the plastron length 2 mm. during that period. When collected May 3 measurements of the growth zone indicated that it had grown 2.9 mm. in the previous season of 1940. It may thus be concluded that this individual did not grow during the last portion of the 1939 season, the winter of 1939-1940, 1940-1941, or the few days it was released in the 1941 season.

Shedding of the Outer Layer of the Horny Plates

The time of shedding of the horny plates affects the annuli and may be correlated with growth. It is necessary to know when and how frequently shedding occurs, what effect it has on the annuli, and whether or not the shedding of the plates stimulates growth. Groups of turtles collected during each month were examined for evidence of recent, present, or near future shedding, and a number of individuals were marked with enamel on the carapace and released in the hope of recovery.

The chronological distribution of the records of shedding indicates that it takes place mainly in late summer but that it may occur during other periods. Some turtles were found shedding during each month in which adequate samples were taken (table 3).

Ewing (1939:88) states, "Many turtles at the time of molting cast the

TABLE 2.—Comparison of growth determinations as made by recovery records and annuli measurements.

No.	Sex	Dates of release and recovery	Total days released	Total days in growing season	Growth determined from recovery records	Days in growing season represented by rings	Growth determined from all plate annuli	Growth determined from pectoral plate annuli
					mm.		mm.	mm.
150	j	6/18/39–2/11/41	603	257	21	306	21	21
155	j ♀	8/19/39–6/30/40	315	103	9	61	9	8
212	♀	7/27/39–5/ 3 /41	645	221	4	153	4	3
215	j	7/27/39–9/17/40	417	65	3	153	11	10
232	j ♂	8/ 1 /41–9/ 1 /42	396	184	29	123	27	27
236	j ♀	7/28/39–5/ 3 /41	644	220	2	153	3	2
244	j ♀	7/30/39–4/25/41	634	215	24	306	32	32
269	j ♀	8/ 9 /39–8/11/41	732	308	9	103	9	6
273	j	8/ 9 /39–5/ 3 /41	632	208	6	153	7	8
310	j ♀	8/11/39–4/25/41	622	203	3	153	3	5
315	j ♀	8/11/39–8/ 1 /41	720	296	6	193	8	6
318	j ♀	8/11/39–5/ 6 /41	633	209	9	153	7	2
356	j	8/26/39–8/18/40	357	145	1	110	4	3
430	j	9/11/39–6/ 5 /41	632	208	14	153	14	..
439	j	9/16/39–2/21/41	523	188	26	153	25	..
480	j	3/23/40–5/14/41	417	167	4	153	7	6
497	♀	5/19/40–4/25/41	341	134	3	153	4	2
544	j ♀	5/18/40–5/ 5 /41	352	140	2	153	5	5
562	j	5/30/40–4/25/41	330	123	3	153	7	4
638	j	6/30/40–5/23/41	327	114	12	153	19	23
664	♂	7/ 2 /40–5/ 3 /41	305	93	2	90	2	..
691	j	7/10/40–5/23/41	317	105	6	153	7	8
719	j	7/27/40–8/ 6 /41	375	163	8	98	9	10
813	j	9/18/40–8/ 6 /41	322	110	7	98	5	5
1773	j	3/31/41–9/ 7 /42	525	283	23	283	24	26
2345	j ♀	5/ 3 /41–8/ 6 /41	95	95	6	98	7	8
2396	j	5/14/41–7/ 3 /42	415	203	26	68	19	17
2412	j	5/15/41–9/ 1 /42	474	262	17	124	21	..

See page 727 for key to abbreviations used in the above table.

outer layers of the dermal shields. These usually come irregularly at the time of the general molt, which takes place in the early part of the summer. At times however, the old horny layers do not loosen and may not be cast for two or more years."

Of the turtles marked, painted with enamel on the carapace, and released,[4]

[4] There is of course some possibility that the enamel on the carapace may interfere with normal shedding but as in some cases recovered individuals were molting enamel-coated plates with no difficulty, we may at least assume that the enamel does not prevent shedding.

none of 9 released in October of 1938 had shed during the release period, but 2, No. 30 and No. 15, were in the process when recovered. There was no paint present on the scutes of No. 15, and it was thus not certain that this was its first shedding since its release. No. 30, however, still retained paint on the molting plates. The seven turtles that did not shed were at liberty from 200 to 652 days. The turtles released July 10, 1940 and recovered in 1940 and 1941 were very different in this respect. Of 23 releases, 19 shed during the period of release, which varied from 24 to 397 days. The 4 turtles that did not shed were re-collected in the first few days of the following May. Two had shed just previous to the time of their release, but it was not possible to determine if the other 2 had recently shed.

TABLE 3.—The occurrence of shedding.

Month	No. not molting	No. molting	Per cent molting
January	0	0	0
February	18	0	0
March	1,101	102	8
April	28	0	0
May	251	3	1
June	451	17	4
July	65	21	24
August	310	24	7
September	27	13	33
October	120	11	8
November	5	0	0
December	0	0	0

See page 727 for key to abbreviations used in the above table.

These two sets of data indicate that shedding may occur more frequently in young turtles than in old, as all of the individuals released in 1938 had passed the stage of rapid growth but all of those, except possibly Nos. 675, 699, 700 and 695, released in 1940 were comparatively young turtles. Older turtles, furthermore, have thickened horny plates that are never found in the young.

This observation might lead one to the assumption that shedding is a function of growth of the shell, but such assumption is not clearly justified by the growth records. Only 11 of the 19 individuals that shed their plates in the interval of release showed actual increase in length, and 5 of 11 turtles that did not shed did show some growth. All 5 of these are in the first group (old turtles), and in the second group (younger turtles) the 4 that did not molt showed no growth.

Pearse (1923:147) suggests that differences in individual growth in *Chrysemys* are probably correlated with shedding, growth being thought to be rapid immediately after the plates are lost. There is no evidence in support of

this view from this present study. Of 14 turtles known to have shed near the time of capture, only 7 grew in the subsequent period of release. Thus, there appears to be little reason for inferring rapid growth immediately after shedding.

Shedding has no effect on the actual formation of the growth rings but does change their appearance. When the layer of epidermis extending over the entire scute, including the new growth zone, is shed, the outline of the rings formed in previous seasons is weakened. Successive shedding presumably accounts for the elimination of the growth rings in older turtles (pl. 3).

Analysis of Growth

Other students of growth in turtles have stated its amount in terms of increase in length of carapace or of total weight. These were found to be less satisfactory as a measure of growth in *Pseudemys* than increase in plastral length. The plastron appears to be less affected by changes in the height or curvature of the carapace than any of the 5 shell measurements made; and in addition the plastral annuli, formed in a closer approximation to a plane, are more usable as a measure of growth than those of the carapace. The plastral length is used here as a measure of the size of the turtle, and growth is discussed in terms of plastral length only.

Absolute growth in plastral length was determined through release-recovery records, annulus measurements, and measurements of the plastron. Measurements of annuli were made on 717 individuals; 621 juveniles, 42 males and 54 females. Of these, 177 had 2-4 rings representing 2 to 5 successive seasons of growth. Plastral length measurements were made on 2880 turtles. Of 1985 turtles marked and released, 466 were recovered 1-5 times, with a total of 603 instances of recovery.

In the method of release and recovery, an increase in length of 1 mm. or more is the minimum that can be detected. Turtles showing no increase in measurements may have grown a fraction of a millimeter, or not at all. Growth ring measurements could not, in most individuals, be used to measure an increase in length of less than 2-3 mm. A small increase in total length of the plastron makes such a slight difference in the individual growth zone of the component plates that they cannot be accurately measured. Thus the lowest point in the range of growth as determined by ring measurements must be expected to be higher than that determined by release-recovery records; and the percentage of turtles showing no measurable growth on the basis of plastral annuli will be greater than the percentage making no measurable growth as determined by release-recovery procedure.

As age cannot be determined adequately for most individuals, and no distinct natural size groups are apparent in turtles over one season old, growth must necessarily be discussed in terms of arbitrarily selected size groups of juveniles, males and females. The sex of juveniles cannot be satisfactorily determined without dissection, and they are here considered as a group.

The secondary sex characters of the male (elongated nails on fore foot, long preanal area, narrow head, melanism) do not appear until the individual reaches a length of 85-110 mm. (Cagle, 1945). For convenience in handling

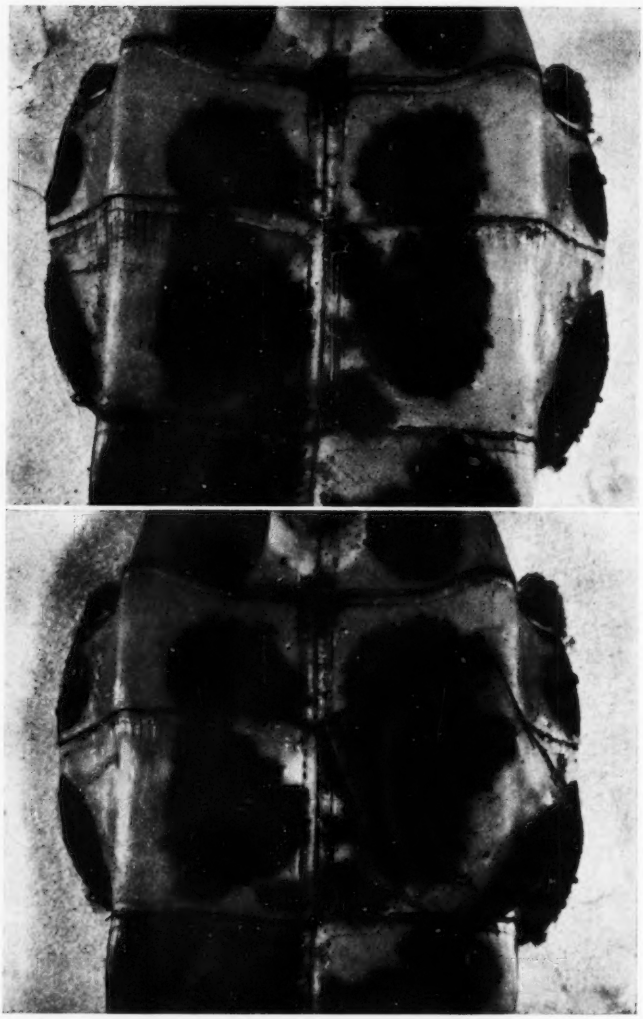


PLATE 3.—The effect of shedding on the growth rings and the growth zones.

Upper. The plastron of a female collected July 4, 1941; plastron length 215 mm. The left abdominal plate shows two distinct growth rings. The light zone outside the last formed ring represents growth during the period May 1 to July 4, 1939.

Lower. The scute of the left abdominal plate has been shed. Note the change in the appearance of the growth rings which is now not distinct enough to be accurately measured.

and presenting data, I have selected the measurement of 100 mm. from this range as that size above which the great majority of males are sexually mature.

The female slider turtle becomes sexually mature at a plastral length of 165 to 195 mm. (Cagle, 1944c). All females larger than 165 mm. are here considered sexually mature.

The data for all release-recovery records and ring measurements have been consolidated in the form of tables and graphs.

THE FIRST SEASON OF GROWTH

The turtles hatch in the latter part of August or the early part of September in southern Illinois but do not usually leave the nest until the following spring. During the period in the nest there is a gradual resorption of the yolk accompanied by closure of the umbilicus and a general stiffening and hardening of the carapace and plastron. There is also a reduction of the height and an increase in the length and width of the shell. The hatchlings may leave the nest and enter the water during late March, April or early May (Cagle, 1944d).

These turtles may find the temperature still below that of their activity threshold. Such individuals float idly near the surface or cling to masses of vegetation until the temperature rises.

During the period of inactivity there is a continued reduction of the yolk mass. Two turtles collected April 27, 1940 contained yolk balls measuring 8 x 5 mm. and 4 x 3 mm. respectively. Of 21 turtles, collected May 22 to May 31, none showing any evidence of growth, 5 had no yolk present and 16 contained yolk balls 1 mm. in diameter to 2 x 6 mm., mean size 2 mm. in diameter. Three of 11 first season turtles collected June 6, 1940 had not grown and all had yolk balls approximately 1 mm. in diameter.

There is some question as to whether the yolk actually provides nourishment for the young turtle. Hildebrand and Hatsel (1926:14) believes that it does. In all the hatchlings of 7 species that I have examined the yolk is retained as a globular mass attached to the intestine and is not contained in the stomach. The researches on yolk utilization in chicks (Parker, 1929) suggest that the yolk mass may not serve as a source of nutrition. Turtles frequently feed before the yolk is completely reduced. Hatchlings collected throughout May often contained yolk balls when the intestine and stomach were filled with food.

Hatchlings showing development of plastral growth zones were first collected May 22-25, 1941, when 4 of the 44 turtles from City Lake and 18 of 20 collected at Lovett Pond showed evidence of growth, none of 17 collected from Thomas Pond, May 14, 1941 had grown. Of 11 turtles in their first season of growth collected June 6, 1940 from City Lake, 3 had not grown, 5 had grown very little, and the other 3 had grown 5.9, 4.8, and 6.9 mm. respectively. These data indicate that although growth may begin in May, the time of its initiation may vary widely in different water bodies as well as in individuals living in the same surroundings.

The annulus measurements of 60 hatchlings collected during the growing season from City Lake indicate that growth may be rapid and continuous

throughout the first season (fig. 4). The mean growth increments for the first 3 months were 4.0 mm., 6.3 mm., and 4.3 mm. A single turtle taken in September does not give a satisfactory basis for the approximation of growth increments during the last two months of the growing season. A sample of 12 collected in October showed a mean increment for the season of 25.4 mm. This is somewhat higher than the first season growth computed from the records of 55 other individuals that had completed one season of growth (table 4, fig. 8). These records indicate that the first season increase of individuals in City Lake ranges from 4.8 to 35.2 mm., mean growth 18.7 mm.

Annulus measurements indicative of the complete first season of growth are available on 31 other individuals, 11 from the Drainage Ditch and 20 from Lovett Pond. These groups had rates of growth different from that of the series from City Lake (table 4, fig. 8). The 20 turtles from Lovett Pond had grown less than one-half as much (1.9-14.8 mm.; mean, 8.75±.70) as those from City Lake and less than one-third as much as those from the Drainage Ditch (19.1-42.1 mm.; mean 27.5±1.92). These data demonstrate that habitat may have a highly significant effect on growth rate.

TABLE 4.—Comparison of first season growth in turtles from three areas. Based on ring measurements of individuals having completed one season of growth.

Area	No.	Range	S.D.	Mean	S.E.
Drainage Ditch	11	19.1–42.1	6.38	27.5	1.92
City Lake	55	4.8–35.2	7.70	18.7	1.03
Lovett Pond	20	1.9–14.8	3.16	8.75	0.70

See page 727 for key to abbreviations used in the above table.

The first season growth of the Drainage Ditch turtles (fig. 7; Nos. 2898, 890, 995) was more rapid than that of City Lake turtles for the same year (fig. 5; Nos. 826, 827, 539, 844), and a similar difference is apparent for the 1938 season.

Two other sources of information on the first season of growth are the annulus measurements indicating a part of a season's growth (Table 6) and the release-recovery data (table 7). The amount of growth during the first season is best measured by the mean increment per 100 days of the first 2 size groups (20-30 and 30-40 mm.). The release-recovery records denote an increment of 13 mm., or a 43% increase; the ring measurements an increment of 14.4 mm. or a 48% increase.

The ring measurements of Drainage Ditch hatchlings indicate an increment of 15.8 mm. or a 53% increase. Lovett Pond turtles grew only 5.6 mm. per 100 days or a 19% increase. No release-recovery records are available on first season turtles in the Drainage Ditch or Lovett Pond.

The time of initiation of first season growth may be of major importance

in explaining the wide difference of increment in these 3 areas. No data are available for 1940 but hatchlings collected during the last week of May 1941 indicate that the time of growth initiation does vary in different areas. Of 40 turtles collected in City Lake only 2 exhibited measurable growth; of 15 from the Drainage Ditch, none had grown; of 20 from Lovett Pond, 17 had grown.

We might conclude that turtles from the Drainage Ditch exhibit a higher growth increment than turtles from the other two areas; but if the ring measurements of 4 first season turtles examined in 1942 be considered, a modification of this conclusion is necessary. The data on these 4 turtles (table 9) indicate a growth of 12.5-38.6 mm., mean 28.5 mm. per 100 days of the 1942 season, a growth rate substantially different than that based on ring data of

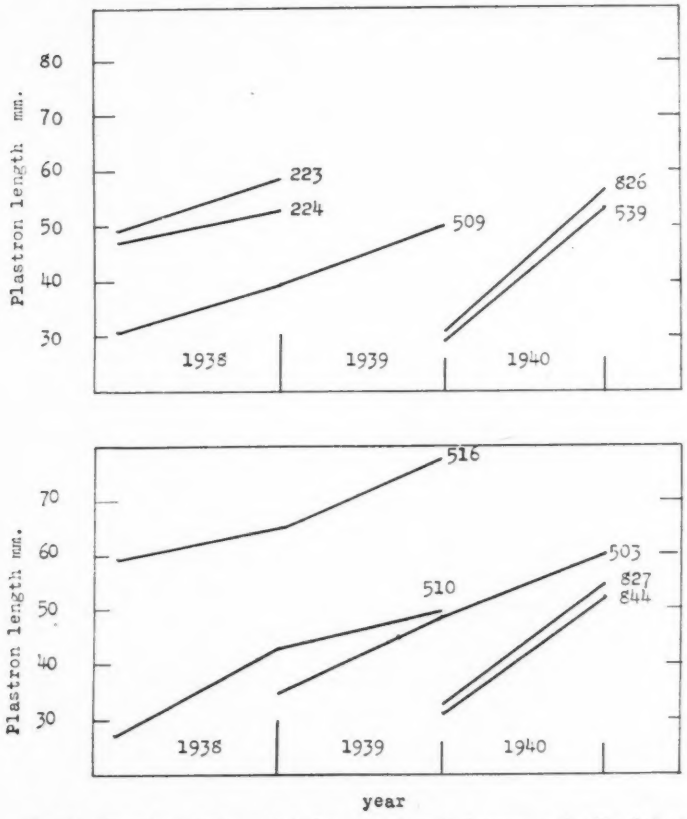


Fig. 5.—Growth of turtles in their first, second or third season at the City Lake in 1938, '39, '40.

turtles collected previous to 1942 (mean 14.4 mm. per 100 days). This increase resulted from a radical change in the biota of City Lake in 1942, subsequently discussed in this report. Thus previous to the 1942 season the Drainage Ditch turtles did have a higher rate of growth than those in City Lake but in 1942 this situation was reversed. This greater growth in the Drainage Ditch previous to 1942 was, presumably, a result of the wealth of invertebrate life present in and along the margins of the ditch. The narrow vegetation-crowded, shallow portions inhabited by the young turtles are overhung by weeds that supply a rain of terrestrial insects, which provide the main item of the young turtle's food. Such an abundance of food was not present in City Lake but would be

TABLE 5.—Growth of City Lake turtles per season. Based on annuli measurements indicating one complete season's growth.

	Juveniles			Males		
Size group mm.	No.	Inc. Range mm.	Inc. M.	No.	Inc. Range mm.	Inc. M.
20–30	14	10.4–33.5	20.1			
30–40	43	4.8–35.2	18.6			
40–50	7	5.5–18.0	9.3			
50–60	12	6.2–18.8	11.8			
60–70	24	7.3–18.9	12.0			
70–80	34	5.6–33.0	12.2	1		5.7
80–90	17	3.6–29.5	11.4	1		7.6
90–100	16	4.6–14.9	11.3	2	12.4–16.0	14.2
100–110	8	6.9–18.1	11.1			
110–120	6	8.6–28.9	15.2			
120–130	9	4.4–20.8	11.0			
130–140	5	7.1–17.5	12.9			
140–150	2	6.9–14.3	10.6			

See page 727 for key to abbreviations used in the above table.

expected in Lovett Pond where in normal times the shallow waters are rich in life. This pond sometimes dries during the summer months and is refilled slowly during the next spring. Such a situation may have existed in 1940; if so, it is the most likely explanation of the low growth rate in the turtles from the pond.

The growth record of a juvenile female collected from Lake Glendale emphasizes the possible influence of habitat on growth; it has only one annulus, (pl. 2) and if the age judgment based on the ring evidence is correct, this turtle had a phenomenal growth for the first season. Its plastron had increased from 31.6 mm. (as indicated by the first annuli) to a length of 110 mm., an increment of 78.4 mm. The annuli of the carapace are as distinct as those of the plastron and also indicate that the turtle is in its second season of growth. The only other explanation of this evidence is that the turtle is much older

than is indicated and has been growing continuously without forming growth zones. This would indicate a habitat in which the temperature remained fairly high and food abundant during the winter. It is difficult to concede the possibility of such a place existing in the lake or the adjacent waters. In addition one would expect the first annuli to be indistinct if the turtle were several years old; yet they were as sharply defined as those of the usual 2-3 year old turtle. Its growth for the second season of its life (47.7 mm. per 100 days) was nearly as rapid as that during the first (51.2 mm per 100 days). Five other larger individuals taken from the lake on the same date also show an unsually rapid growth.

TABLE 6.—The growth of City Lake turtles per 100 days of the season. Based on annuli measurements indicating less than one season of growth.

	Juveniles and females				Males			
Size group mm.	No.	Range mm.	M.	% inc. 100 days	No.	Range mm.	M.	% inc. 100 days
20–30	15	10.7–24.4	16.1	64				
30–40	31	9.1–42.3	16.5	47				
40–50	4	8.4–31.6	16.2	36				
50–60	12	2.5–33.0	12.3	22				
60–70	7	11.2–26.5	20.6	32				
70–80	16	2.3–17.4	9.7	13				
80–90	34	2.9–21.8	8.6	10	1		6.1	7
90–100	26	2.7–23.3	10.5	11	2	6.1– 7.4	6.9	7
100–110	22	2.5–34.0	11.4	10	6	3.2–18.9	8.0	8
110–120	16	3.2–19.7	10.3	9	3	12.3–13.2	12.7	11
120–130	15	2.3–22.2	12.6	10	1		8.0	6
130–140	7	8.3–16.7	9.2	7				
140–150	6	5.0–19.5	11.9	8				
150–160	6	2.1–12.4	7.3	5				
160–170	9	4.9–14.3	9.4	6				
170–180	3	3.9–17.0	10.2	6				
180–190	2	6.7– 9.0	7.8	4				
190–200	3	0.7– 7.1	3.7	2				

See page 727 for key to abbreviations used in the above table.

The release-recovery records yielded additional information on first season growth. Of 166 turtles in the size range 20-50 mm., most of which were in their first season of growth, released from August, 1938 to July, 1941, 24 were recovered at least once. Thirteen of these show great individual difference in growth rate. Their growth, during at least 25 days in the growing season, calculated as growth per 100 days, ranged from 0 to 30.6 mm., or from no increase at all to one of 77%. A comparison of the records of individuals released during the same period adds further emphasis to this variation. Nos. 430 and 439 both had the same plastron length and were released for similar

periods. The former grew 14 mm.; the latter, 26 mm. A possible influence on this growth was the fact that No. 430 spent the first winter of its life in the nest and No. 439 in the water. The former, released for the longest period of any turtles in this group, a total of 632 days, encompassing 19 days in the 1939 growing season (spent in the nest), the complete season of 1940 and 36 days in the 1941 season, was one of 6 hatchlings that spent the winter in a nest (Cagle, 1944d). When recovered on June 5, 1941, its ring measurements indicated that it had grown 14 mm. during the 1940 season, the only period in which it had grown. Nos. 2589 and 2627 were released during the same periods in the same portion of the lake. One grew only 1 mm.; the other, 14 mm.

TABLE 7.—The growth of turtles per 100 days of the growing season in City Lake. Determined from records of turtles released at least 20 days and showing measurable growth.

Size group mm.	Juveniles and females				Males			
	No.	Range mm.	M.	% inc. 100 days	No.	Range mm.	M.	% inc. 100 days
20–30	3	6.7–15.5	11.4	46				
30–40	9	1.7–30.6	14.6	43				
40–50	2	5.7– 7.5	6.6	15				
50–60	6	2.4– 8.2	5.4	10				
60–70	7	3.2– 9.6	6.4	10				
70–80	13	1.7–19.4	6.4	9				
80–90	23	0.4– 9.6	2.5	3				
90–100	21	0.7–12.5	3.5	4	3	1.7–18.2	7.3	8
100–110	36	0.8–28.5	4.1	4	10	0.6– 8.3	3.3	3
110–120	29	1.1–11.3	3.6	3	10	0.8– 8.6	2.2	2
120–130	21	0.7–13.1	3.7	3	13	0.6– 3.4	1.7	1
130–140	13	0.8–17.0	4.9	4	8	0.5– 3.1	1.3	1
140–150	13	0.7– 8.6	3.2	2	4	0.8– 2.2	1.6	1
150–160	5	1.0–10.3	7.0	5	5	2.2– 4.7	3.3	2
160–170	7	1.1–11.1	4.4	3	2	1.2– 1.5	1.3	1
170–180	5	2.0– 4.2	2.8	2	1		3.6	2
180–190	6	0.7–13.1	4.6	2	2	1.0– 3.9	2.4	1
190–200	5	0.5– 3.9	1.9	1	1		2.0	1
200–210	6	0.4–15.3	3.6	2				
210–220	1		1.0					

See page 727 for key to abbreviations used in the above table.

Great individual variation is also shown by the ring measurements of turtles from the Drainage Ditch in 1941 (fig. 8). These turtles were collected in about the same section of the ditch and, in all probability, had spent the first season under like ecological conditions. Similar variation of growth in turtles collected in these months is exhibited by the ranges of monthly increments in City Lake turtles (fig. 4).

It is also apparent that hatchling turtles may be isolated in a habitat where food is available for no more than a subsistence diet. Records of young captive turtles indicate that they may live for long periods without growing. Schneck (1886:897) reports keeping a young slider turtle in confinement for more than two years during which it ate freely but made no perceptible growth.

In view of the great individual variation in growth, one would not expect distinct size groups to be apparent in young turtles. One sample of 119 turtles,

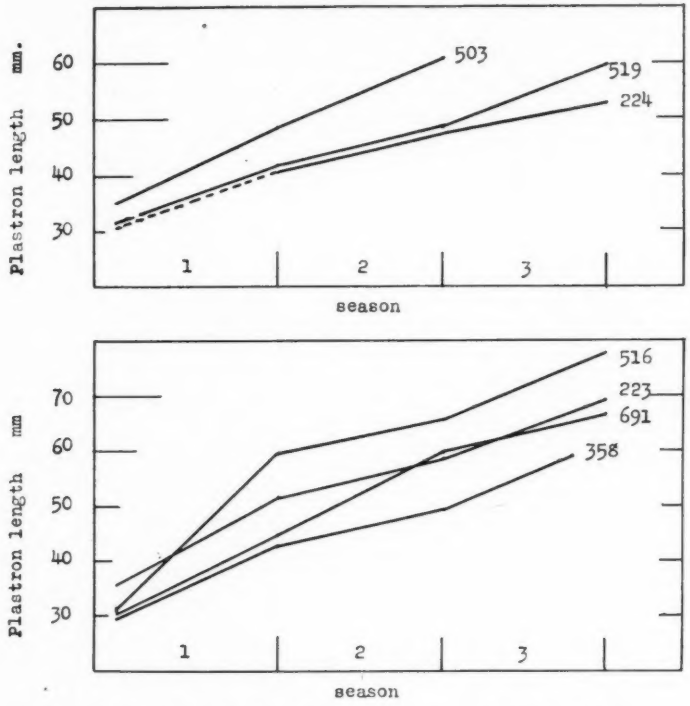


Fig. 6.—The growth of turtles in their first three seasons at the City Lake.

collected from a mudflat at City Like, June 14-20, 1941 was studied for evidence of size groups (fig. 3); five such groups are apparent, but they do not represent age groups. The age of 42 turtles in the first 3 size groups was determined; it was possible to determine the age of only one of the individuals with a plastron length greater than 64 mm. Of the first size group 30 were in their first season of growth. The second size group contained at least five individuals in their second season of growth and 3 in their third. Four of those falling in the third size group were 3 seasons old and one was 5 seasons

TABLE 8.—Summary of the growth of City Lake turtles per 100 days.

Size group (mm.)	Juveniles and females						Males					
	Release-recovery		Ring measurements less than 1 season		Ring measurements 1 complete season		Release-recovery		Ring measurements less than 1 season		Ring measurements 1 complete season	
	Increment (mm.)	% inc.	Increment (mm.)	% inc.	Increment (mm.)	% inc.	Increment 100 days (mm.)	% inc.	Increment 100 days (mm.)	% inc.	Increment 100 days (mm.)	% inc.
20–30	11.4	46	16.1	64	13.1	52						
30–40	14.6	43	16.5	47	12.1	35						
40–50	6.6	15	16.2	36	6.1	14						
50–60	5.4	10	12.3	22	7.7	14						
60–70	6.4	10	20.6	32	7.8	12						
70–80	6.4	9	9.7	11	8.0	11					3.7	5
80–90	2.5	3	8.6	10	7.5	9			6.1	7	4.9	6
90–100	3.5	4	10.5	11	7.4	8	7.3	8	6.9	7	9.2	10
100–110	4.1	4	11.4	10	7.3	7	3.3	3	8.0	8		
110–120	3.6	3	10.3	9	9.9	9	2.2	2	12.7	11		
120–130	3.7	3	12.6	10	7.2	6	1.7	1	8.0	6		
130–140	4.9	4	9.2	7	8.4	6	1.3	1				
140–150	3.2	2	11.9	8	6.9	5	1.6	1				
150–160	7.0	5	7.3	5			3.3	2				
160–170	4.4	3	9.4	6			1.3	1				
170–180	2.8	2	10.2	6			3.6	2				
180–190	4.6	2	7.8	4			2.4	1				
190–200	1.9	1	3.7	2								
200–210	3.6	2										

See page 727 for key to abbreviations used in the above table.

old. It is apparent that only the first size group represents an age group. The variation in individual growth rate results in a wide overlap in size of individuals differing several years in age.

THE SECOND AND THIRD SEASONS OF GROWTH

The only data on the second and third seasons of growth are derived from the records of those individuals that have retained 2-4 sets of annuli. From measurements of these the growth for the first 3 seasons may be determined.

The ring measurements of 7 Drainage Ditch turtles (table 10) indicate a mean growth of 15.8 mm. for the second season and 14.5 mm. for the third.

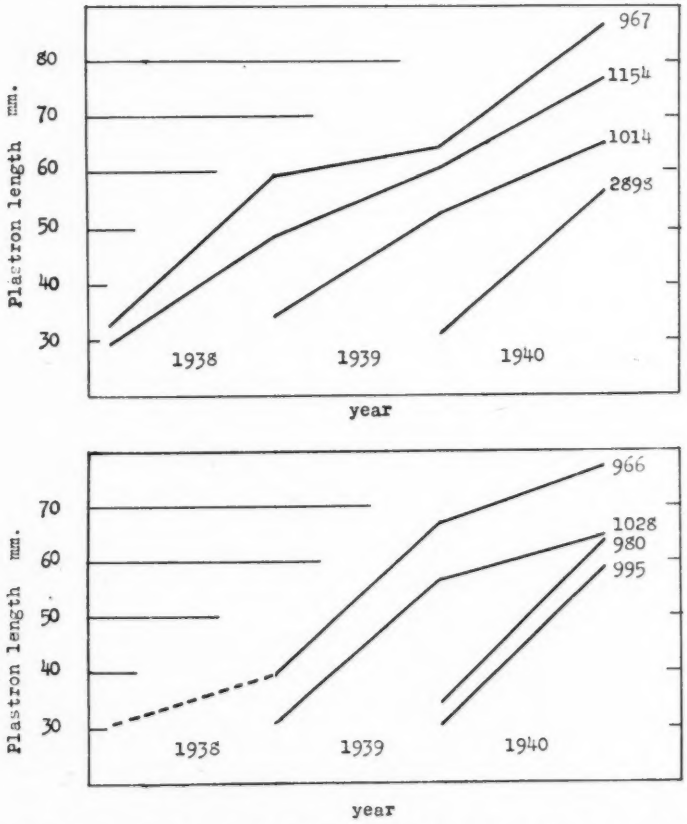


Fig. 7.—Growth of turtles in their first, second or third season at the Drainage Ditch in 1938, '39, '40.

The records of 7 City Lake turtles indicate a mean growth of 8.2 mm. for the second season, and a slightly larger amount, 10 mm., for the third (table 10).

Both sets of data indicate a smaller increment for the second season than for the first, and the records of some individuals from the Drainage Ditch and 4 from City Lake show greater increments during the third season. These increases are not as would be expected on the basis of the decreasing increment with increasing size (tables 8, 9). A difference due to the conditions of a particular season is thus suggested.

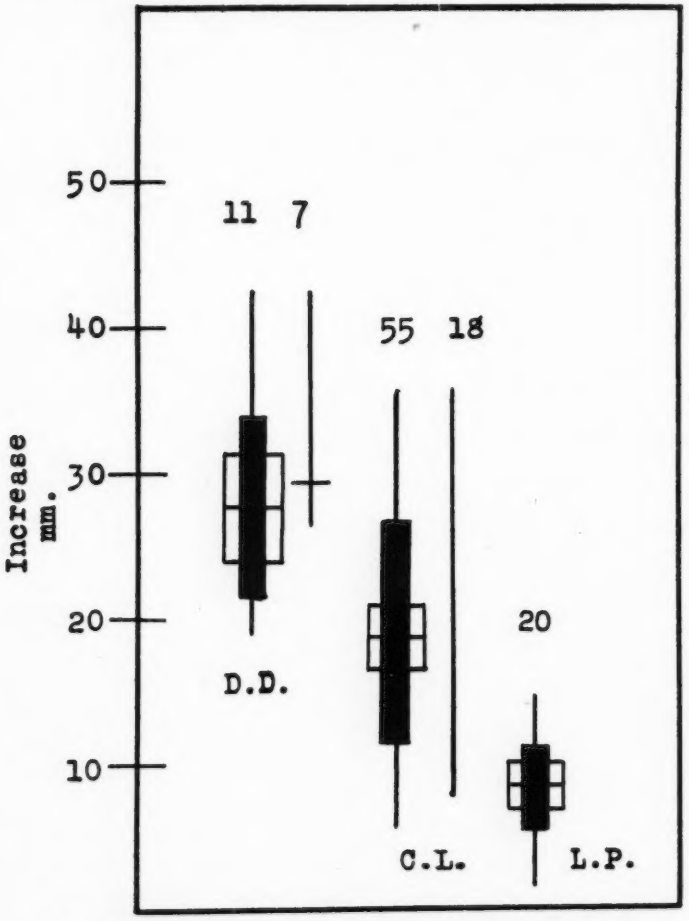


Fig. 8.—The comparison of growth in three areas during the first season.

All of the records of third season growth except that of No. 691 (fig. 6) represent growth in the 1938 season. The growth records of other turtles during this period (fig. 5) do not suggest that this season was unusually favorable for growth. All of the third season growth records of the ditch turtles represent growth for 1940, and the records of turtles released during this year (fig. 7) suggest that it may have been exceptionally favorable for growth. Thus a partial explanation is provided for these greater increments for the third season.

TABLE 9.—Growth of turtles per 100 days of the 1942 season at City Lake. Based on annulus measurements from juveniles and females.

Size group (mm.)	No.	Range (mm.)	M. (mm.)	% inc. 100 days
20–30	2	12.5–38.6	25.5	87
30–40	2	30.3–32.7	31.5	90
70–80	1		30.2	40
80–90	6	19.1–31.0	27.1	32
90–100	6	15.0–32.9	24.8	26
100–110	6	8.6–29.4	15.8	15
110–120	3	15.0–21.9	17.3	15
120–130	1		32.7	26
130–140	1		18.2	14
140–150	1		12.8	9
150–160	1		15.4	10
160–170	1		1.9	1

See page 727 for key to abbreviations used in the above table.

Eight of 9 turtles collected June 14, 1941 were in their second season of growth, but none showed any signs of a second season growth zone. The first annuli were evident in all.

THE GROWTH OF JUVENILES OF UNDETERMINED AGE

Since the age of the great majority of turtles cannot be determined it is necessary to discuss their growth in terms of arbitrarily selected size groups. A juvenile is here considered to be any turtle having a plastron length less than 165 mm. and not showing the secondary sex characteristics of the male.

The release-recovery records of 33 juveniles released at City Lake show considerable variation in growth rates. No. 149, spending 39 days in the 1939 growing season grew 3 mm.; but in the next 1044 days (of which 408 were in growing seasons) it grew 28 mm. No. 148, released for 779 days, of which 355 were in growing seasons, increased 14 mm. in length. No. 150 increased 21 mm. in 257 days of growing season. No. 565 increased 13 mm. in 216 days. Contrary to expectation the juvenile (No. 127) that grew at the greatest rate per 100 days (11.3 mm.) was a comparatively large turtle. This individual, at liberty for 788 days of which 364 were in growing season (a portion of

the 1939, all of the 1940, and the first portion of the 1941 season), was 113 mm. in length when first released.

Although most of the juveniles released for 100 or more days in the growing season grew comparatively rapidly, some were obviously slow-growing. For example No. 480 increased only 4 mm. in 167 days of growing season. Another, No. 230, grew only 4 mm. in 205 days. Recovered twice after this record, it showed no additional growth after one period of 238 and another of 22 days. No. 231, in a period of 739 days of which 315 were in growing season, grew only 3 mm.; and No. 262, in 674 days, 250 in the season, grew only 1 mm.

TABLE 10.—Growth of turtles at the Drainage Ditch during the first 3 seasons. *Based on annuli measurements.*

No.	Plastron length at birth (mm.)	Inc. first season (mm.)	Inc. second season	Inc. third season
171	32.2	26.6	24.4	.....
966	30.1	7.8	29.3	11.5
967	32.5	27.4	14.4	14.6
995	30.9	27.4	10.1	.....
1014	34.1	19.7	12.3	.....
1028	31.3	23.4	7.7	.....
1154	29.3	19.4	12.2	17.5

Growth of turtles at City Lake during the first 3 seasons. *Based on annuli measurements.*

223	35.9	13.0	9.3	11.0
224	30.1	10.0	7.0	5.5
358	29.6	12.7	6.8	12.8
516	31.6	28.1	6.2	12.1
519	31.8	8.6	7.9	11.2
691	30.5	14.1	14.6	7.4
2599	29.2	23.9	6.1	.....

See page 727 for key to abbreviations used in the above table.

These records can but be compared by reducing them to an arbitrary standard of time interval. The growth of all City Lake juveniles was computed as growth per 100 days of the growing season (table 7). It was found that each successively larger group has a smaller increment and thus a correspondingly smaller percentage increase in length. This decline in growth rate is most rapid in the first 7 groups in which the average increment drops from 11.4 mm. to 2.5 mm. The maximum growth per 100 days of the season, 30.6 mm., was made by an individual in its first season of growth. Those groups in the 80-150 mm. range show a somewhat uniform increment. Of 246 juveniles

released 20 or more days in the growing season 45 (18%) showed no detectable increase. The percentage of juveniles not showing increase is highest (44%) in the size group 150-160 mm. and lowest (0%) in the groups 20-30 and 40-50 mm.

The release-recovery data available for Drainage Ditch turtles demonstrate that they have a higher rate of growth than those of City Lake. The most rapidly growing individual (No. 2297), released for 525 days, grew 31 mm. in the 283 growing season days. None of 7 juveniles grew less than 18 mm. in 283 days or 6.3 mm. per 100 days.

A comparison of the records of 2 of the larger juveniles with a sample from City Lake shows that those in the same size range (130-160 mm.) grew an average of 4 mm. in City Lake and an average of 8.7 mm. in the Drainage Ditch (table 11).

TABLE 11.—Growth per 100 days of the growing season as calculated from release-recovery data. (Turtles 130-220 mm. in length).

Sex	City Lake			Drainage Ditch		
	No.	Range (mm.)	Mean	No.	Range (mm.)	Mean
j j	24	0.5–17.0	4.0	4	6.3–10.9	8.7
♀ ♀	31	0.3– 9.2	3.9	11	0.3–14.2	4.2
♂ ♂	19	0.5– 4.7	2.3	5	0.7– 6.0	2.8

See page 727 for key to abbreviations used in the above table.

Annulus measurements were also used in the analysis of juvenile growth (tables 5, 6, 8, 9). A greater number of turtles showing little growth is to be expected in the larger size groups and thus annulus measurements are comparatively few in these groups. That the minimum growth for each size group above the 30-40 mm. group is zero, each successively larger group having a greater number showing no growth, is suggested by a sample from the Drainage Ditch.

None of the City Lake turtles with a length greater than 150 mm. showed sufficient growth to be detected by ring measurements. The increments for each size group for one complete season are quite uniform in those turtles larger than 60 mm. (increment average range from 10.6 to 15.2 mm. in the plastral size range 50-150 mm.). The individual showing the maximum increase for one season (35.2 mm.) was in its first season of growth.

Ring data for a complete season's growth in turtles from the Drainage Ditch (table 12) indicate a higher increment in most size groups than for comparable ones in City Lake. That large turtles in the Drainage Ditch continue to grow relatively rapidly is indicated by the fact that those with lengths greater than 160 mm. (adult females) continue to form distinct rings. This is in decided contrast with the situation in City Lake. This difference is fur-

ther demonstrated in the higher maximum increments in most of the Drainage Ditch size groups.

The data on turtles from City Lake in terms of growth per 100 days of the season determined by ring measurements are somewhat different from those based on release-recovery procedures (table 8). As expected, the ring data, because of the limitation on minimums determined, indicate higher increments for each group than do the release-recovery data. Each series does, however, demonstrate the change in rate in the first few size groups. Thus on the basis of release-recovery data the 46% increase in the size group 20-30 mm. decreases to 9% in the 70-80 mm. group. Succeeding groups of juveniles show a continued percentage decrease (2 to 5%). The two other sets of data show a similar trend.

The annulus measurements of Drainage Ditch turtles were also arranged on the basis of growth per 100 days of the season (table 12). These data may be compared with those computed by the same method for City Lake turtles (table 8).

THE GROWTH OF MALES

The release-recovery records of males in both City Lake and the Drainage Ditch suggest that their growth is slower than that of juveniles and females of the same size. Of 82 males released 20 or more days in the growing season 23 (28%) did not grow one millimeter; 45 (18%) of 246 juveniles and 12 (28%) of 42 adult females did not grow one millimeter. The growth records of adult males (table 8) indicate an average increase per 100 days of the growing season of 2.7 mm. The average growth of juveniles for a similar period was 6.5 mm.; of females 3.2 mm. (table 8). The ring measurements yield a similar result (tables 5, 6, 9, 12).

The maximum growth as determined by release-recovery methods for an adult male in City Lake was 8.6 mm. per 100 days of the season. This is considerably higher than the maximum (5.6 mm.) displayed in 7 males released in the Drainage Ditch.

The mean growth based on release-recovery records of males at City Lake was 1.8 mm. per 100 days; of males at the Drainage Ditch 2.7 mm. Of 82 males released for 20 or more days in the growing season at City Lake 23 (28%) did not grow; of 398 Drainage Ditch males examined for growth by annulus measurements 295 (74%) had no evidence of growth, 79 (20%) had grown slightly, 24 (6%) showed measurable growth.

The percentage of the Drainage Ditch males showing no evidence of growth in the plastral annuli increases in successively larger size groups. Thus in the group 100-110 mm., 21% showed no growth, 29% slight growth, and 50% distinct growth; in size group 160-170 mm., 84% showed no growth, 14% slight growth, and only 2% distinct growth. None of the males larger than 190 mm. yielded evidence of recent growth. The decline of growth rate in the larger males is also demonstrated by all other records (tables 8, 13).

The release-recovery records of some individuals are of special interest. One, released 664 days, of which 240 were in growing season, grew only 2 mm. Another, released 740 days, 316 in growing season, grew only 1 mm.

Some adults grew as rapidly as some juveniles of the same size. One of 112 mm. plastral length, grew 13 mm. in 784 days, 360 of which were in the season. No. 302, 125 mm. plastral length, grew 7 mm. in 725 days, of which 302 were in the growing season.

These data also suggest differences in growth from season to season. No. 396, recovered 3 times, did not change in length during the first 625 days (201 in growing season) but grew 2 mm. in the following 84 days. No. 285 recovered 3 times, did not grow during 2 periods of 111 and 80 days in season, but in a subsequent period of 48 days it increased 2 mm.

All of the males released in the Drainage Ditch grew at least 2 mm. in the interval of release (minimum 93 days in season). They ranged in growth .7 mm. to 5.6 mm. increase on the 100-day basis.

The growth records of males at City Lake show a 3 to 8% increase in length per 100 days in the 85-110 mm. group and a subsequent drop in larger males to a 1 to 2% increase per 100 days of the season (table 8). It should be reemphasized that these data represent measurable growth and do not include the great number showing less than 1 mm. increase.

THE GROWTH OF FEMALES

Adult females were few in City Lake and recoveries were correspondingly rare. The 42 records available show a wide range in growth (table 5) per 100 days of the growing season. Of these, 12 did not grow when released 20 or more days in the growing season; the maximum growth per 100 days of the season was 15.3 mm. The mean increments of almost every size group are higher than those of males of the same groups and lower than those of juveniles. The maximum percentage increase per 100 days (3%), was based on individuals of which some may have been immature. Groups larger than 170 mm. showed 1 to 2% increase.

The release-recovery data on some females indicate that an individual may exhibit radical differences in growth in different seasons. No. 20 grew 4 mm. in 166 days, most of which were in the 1939 season and 2 mm in 106 days of the 1941 season but showed no detectable increase during 114 days of the 1940 season. Similarly another, No. 75, grew 14 mm. in only 91 days of the first part of the 1939 season but only 1 mm. in 61 days of the latter part of the same season.

Six females released at the Drainage Ditch for 535 days, of which 283 were in growing season, all showed a similar growth rate to those in City Lake. The increase for the 283 days ranged from 1 to 9 mm. or from approximately .4 mm. to 3.2 mm. per 100 days of the season.

The few ring measurements (tables 5, 6) available on females from City Lake indicate again a lower rate of growth than for juveniles (2 to 8% increase per 100 days for the females, 9 to 64% for juveniles). The ring measurements of the Drainage Ditch females show a like difference in rate (2 to 5% increase in females, 7 to 52% for juveniles).

Of the 408 females examined for growth on the basis of rings in the Drainage Ditch, 45% showed no evidence of growth, 45% had grown slightly and 10% exhibited measurable growth.

TABLE 12.—Growth of Drainage Ditch turtles. Based on annulus measurements indicating one complete season's growth.

Size group	Juveniles and females					Males				
	No.	Inc. per season range (mm.)	Inc. M.	Inc. per 100 days (mm.)	% inc. per 100 days	No.	Inc. per season range (mm.)	Inc. M.	Inc. per 100 days (mm.)	% inc. per 100 days
20–30	4	19.1–26.3	17.5	11.4	46					
30–40	11	16.2–42.1	27.7	18.1	52					
40–50	4	12.2–21.4	17.0	11.1	25					
50–60	9	4.4–15.9	11.7	7.6	14					
60–70	28	3.0–39.0	14.9	9.7	15					
70–80	38	1.7–31.6	14.7	9.6	13					
80–90	59	3.4–33.0	12.0	7.8	9	2	10.6–19.5	15.0	9.8	12
90–100	43	2.6–34.2	11.0	7.2	8	9	7.6–18.0	13.1	8.5	9
100–110	25	3.5–44.2	12.3	8.0	8	4	1.6–16.8	9.4	6.1	6
110–120	28	0.4–32.0	12.1	7.9	7	2	5.1– 7.1	6.1	4.0	4
120–130	22	3.7–30.5	13.7	8.9	7					
130–140	19	0.9–40.7	17.0	11.1	8	1		19.2	12.5	9
140–150	20	1.6–40.3	15.1	9.9	7	4	7.1–13.7	9.4	6.1	4
150–160	5	0.5–32.4	14.6	11.7	8	1		10.6	6.9	5
160–170	3	15.1–22.7	17.8	11.6	7	2	10.1–10.5	10.3	6.7	4
170–180	10	7.0–24.4	12.4	8.1	4					
180–190	8	7.4–19.3	11.7	7.6	4					
190–200	4	9.1–18.0	14.1	9.2	5					
200–210	2	1.9–12.1	7.0	4.6	2					

See page 727 for key to abbreviations used in the above table.

Discussion

Differences in the growth rate of turtles, occupying different habitats are conspicuous (table 4, fig. 8). The population of the Drainage Ditch consisted of turtles growing at a faster rate than those of City Lake, and the average size of the adults of the ditch population was larger than the average size of the adults in the lake population (mean size of males: 161 mm. in the ditch, 114 mm. in the lake; mean size of females: 193 mm. in the ditch, 180 mm. in the lake). This size difference is a result of the greater age of the population, and of the higher growth rate of the ditch turtles. Individuals of the ditch population move between the ditch and the adjacent ponds, lakes, and swamps as well as the Mississippi River (Cagle, 1944b) and many of the large adults are probably older than the ditch. The greater age of these large turtles is indicated by eroded jaws, thickened horny layers of the carapace, pitted carapace, and almost complete obscuration of color pattern. Comparatively few individuals from City Lake showed evidences of old age.

The greater rate of growth in the ditch turtles is primarily a result of two factors, the shallowness of the water with resultant higher temperatures, and the wealth of available food. Although the water level of the ditch may become very low so that portions of its bed become dry in late summer, there are usually several inches to a few feet of water in the ditch during most of the growing season. The shallow water remains quite warm, and the metabolic rate of the turtles inhabiting it is therefore undoubtedly higher than those of the turtles in City Lake.

The great variation in growth of individuals in each region may result from the fact that individual turtles tend to remain in a given section of the ditch or the lake until forced to move by radical ecological changes. I have demonstrated (1944b) that City Lake supports 3 population groups, each of which tends to remain in one portion of the lake or the adjacent ponds. Differences in the water temperatures, availability of food, and basking sites may result in different growth rates of individuals inhabiting these areas.

The influence of habitat on growth is further shown by the records of turtles collected from Lake Glendale. These indicate a much greater rate of increase than do those of turtles examined from other region. Analysis of the growth of 10 turtles collected in 1942 indicates that the per cent increase per 100 days in plastral length varied from 4 per cent in a large male to 162 per cent in a juvenile. This lake was first flooded in 1940. Just previous to the closing of the water outlet members of the Illinois Natural History Survey poisoned the small streams emptying into the lake bed. A few of the fishes from these waters survived and the lake was stocked with a small number of fish. The few turtles entering the lake thus had an abundance of food available and little competition.

A single individual from Lake Springfield, in central Illinois suggests that the population there may consist of rapidly growing individuals. This adult female, with a plastron length of 260 mm., was the largest of the turtles examined from Illinois. Although exceptionally large, it had the smooth plates, bright colors, distinct pattern and sharp jaws of a relatively young individual.

It was certainly not near senility as the oviducts contained 20 eggs and the ovaries were heavy and crowded with large follicles.

The effect of a change in habitat on growth was noted when the growth of City Lake turtles was determined for 1942. In October of 1941 the lake reached its lowest level since its construction in 1926. From spillway level

TABLE 13.—Growth records of turtles, recovered during the 1942 season, which indicate growth for previous seasons.

No.	Sex	Date	Days in season	P. l. (mm.)	Inc. (mm.)	Inc. per 100 days (mm.)	% inc. 100 days
128	j ♀	6/ 9 /39		101			
		7/27/39	48	102	1	2.1	2
		5/ 5 /41	223	104	2	0.9	1
		6/ 6 /42	185	116	12	6.5	6
129	j ♀	7/27/39		104			
		7/10/40	135	105	1	0.7	1
		8/ 3 /40	24	105			
		6/ 6 /42	248	116	11	4.4	4
149	j	6/18/39		73			
		7/27/39	39	76	3	7.7	10
		6/ 6 /42	408	104	28	6.9	9
		9/ 9 /42	95	119	15	15.8	15
143	j ♀	6/18/39		117			
		6/ 6 /41	294	156	39	13.3	11
		9/ 9 /42	248	165	9	3.6	2
215	j ♀	7/27/39		117			
		9/17/40	205	120	3	1.5	1
		6/ 6 /42	203	132	12	5.9	5
232	j ♂	7/28/39		65			
		6/16/41	264	74	9	3.4	5
		8/ 1 /41	46	74			
		9/ 1 /42	184	103	29	15.8	2
287	♀	8/12/39		182			
		6/30/40	110	183	1	9.1	5
		6/ 6 /42	129	200	17	13.1	7
315	j ♀	8/11/39		127			
		5/ 5 /41	209	128	1	0.5	4
		8/ 6 /41	93	133	5	5.4	4
		9/ 9 /42	187	143	10	5.3	4
384	j ♀	8/27/39		104			
		6/19/40	84	105	1	1.2	1
		9/11/42	390	143	38	9.7	9

See page 727 for key to abbreviations used in the above table.

(450 acres) in early spring it dropped steadily with slight fluctuation to an average depth of a few inches covering about 10 acres. During mid-October it was drained except for 2 small pools and did not refill to spillway level until April of 1942. During the period of low water vegetation grew luxuriantly on the exposed bottom, and in the spring and summer of 1942 all the shallow areas of the lake developed extensive beds of aquatic plants not previously present in the lake.

During the period when the water level was very low the greater part of the turtle population moved to adjacent ponds and streams but returned when the lake was again flooded (Cagle, 1944b).

The radical change in the amount of vegetation in the lake was reflected by a change in the growth of the turtles. The ring measurements of 31 juveniles indicate that they were growing more rapidly in 1942 than individuals of the same size in the previous seasons. Thus 4 individuals in the 20-40 mm. group (all in their first season of growth) were growing at a rate of 12.5 to 38.6 mm., mean 28.5 mm. per 100 days of the season. Forty-six individuals of the same size range collected in previous seasons grew at a rate of 9 mm to 42 mm., mean 16.3 mm. A faster rate of growth than in earlier years was indicated by the ring measurements of the individuals in each group except the 160-170 mm. one (compare the percentage increase per 100 days of each size group in table 6 with that of each size group in table 9). Furthermore, these turtles were growing more rapidly than those in the Drainage Ditch during previous seasons as is seen by comparison of the percentage increase per 100 days of each size group in table 12 with that of each size group in table 9.

Because of the wide variation of individual growth, the records of these individuals whose growth can be determined for the 1942 season as well as for previous seasons present the better picture of the change in growth rate. Two of the 31 turtles whose rings were studied in 1942 had 2 or more series of rings from which growth for previous seasons could be computed. One, a juvenile female 119 mm. in length, had grown at a rate of 7.8 mm. per 100 days in 1941 but at a rate of 22.5 mm. per 100 days in 1942. A second juvenile, length at time of collection 107 mm., grew at a rate of 6.6 mm. per 100 days in 1937, it first season of growth; a rate of 8.6 mm. per 100 days in 1938; and 8.7 mm. in 1939. In 1942 it grew at a rate of 21.9 mm. per 100 days, a greater rate than in any other season of its life, including the first season when growth is usually the most rapid.

Some of the turtles collected in 1942 had been recovered on previous occasions, and it is therefore possible to compare their growth in 1942 with that of previous years (table 13). The decrease in growth rate of two of these turtles was probably the result of the approach of sexual maturity since the plastron length of the female (No. 143) at the time of collection in 1942 was 165 mm. and that of the male (No. 232) 103 mm. Seven had grown more rapidly in 1942 than in previous years. Some of the rate increases were exceptionally large. In 1939, No. 149 increased in length at the rate of 10% per 100 days; in 1941, at the rate of 9%; but, in 1942, when, on the basis of

the decreasing rate with increasing size previously demonstrated, one would expect a marked decrease in rate, it increased in length at the rate of 15% per 100 days. The growth of these 7 individuals during 1942 was more rapid than that of any other of the same size group in previous years.

These data indicate that radical differences may exist in the growth rate of turtles living in different habitats within a region small enough to have no significant variation in the length of the growing season.

They further suggest that turtles are capable of very rapid growth and that environmental factors affect the rate of increase. The rate of growth responds quickly to a change in environmental conditions.

Summary

METHODS

1. A measuring device suitable for accurate measurement of the carapace and plastron is described.

2. It is demonstrated that measurements of annuli provide valid data for growth analysis, providing growth data for previous seasons, and delimiting the period in which growth, detected by other procedures, occurred.

ANNUAL ACTIVITY CYCLE

3. The normal activity in nature is limited to the temperature range of approximately 10° to 37° C.

4. Turtles are active in the winter only as water temperatures permit. In southern Illinois activity begins about the last of April or the first of May. There is some decline of activity in midsummer and a subsequent increase in August and September. Feeding ceases in early October.

5. The growing season in southern Illinois extends from approximately May 1 to October 1, a period of 153 days.

ANNULUS FORMATION

6. Annuli are usually formed annually and represent the cessation or slowing of growth during the winter months.

7. Annuli are of little value as age indicators since they disappear at a relatively early stage.

SHEDDING

8. Shedding may take place at any time but usually occurs in late summer.

9. Shedding probably occurs more frequently in young turtles than in adults.

10. Shedding has little or no effect on growth.

FIRST SEASON OF GROWTH

11. Growth for the first season is extremely variable. One individual grew only 1.9 mm.; the maximum growth was 78.4 mm.

12. Turtles examined from three areas exhibited radical differences in growth for their first season.

SECOND AND THIRD SEASONS OF GROWTH

13. Growth during the second and third seasons is generally less rapid than during the first, but seasonal differences may reverse this rule.

GROWTH OF JUVENILES (OF UNDETERMINED AGE)

14. There is a progressive decrease in rate of growth with increase in size.
15. Juveniles in each size group exhibit wide variation in the growth rate.

GROWTH OF ADULTS

16. After the attainment of sexual maturity results the growth rate decreases.
17. Growth is very slow in most adults; many showed no evidence of growth when released for long periods.
18. There is a progressive slowing of the growth rate with increase of size.
19. Adult males grow more slowly than females of the same general size.

GENERAL

20. The growth rate is potentially very rapid in juveniles and young adults and is responsive to and limited primarily by ecological factors.
21. Individuals of approximately the same size and living under similar ecological conditions exhibit wide differences in the rate of growth.
22. The largest male collected was 186 mm. in length; mean size of adult males was 135.4 mm. The largest female collected was 260 mm. in length; mean size of adult females was 189.1 mm.

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A KEY TO ABBREVIATIONS USED IN THE TABLES.

C.l.—Carapace length
C.w.—Carapace width
Ht.—Height
Inc.—Increase
M.—Mean
No.—Number of items, or identification number of an individual
P.l.—Plastron length
P.w.—Plastron width
S.D.—Standard deviation
S.E.—Standard error

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Habits of the Swamp Rice Rat, Oryzomys palustris palustris (Harlan)

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Along the South Atlantic coast line, illimitable marshes of swamp grass cover the mud flats of lowlands of the tidal zone (Fig. 1). Here, in the cover of dense vegetation, rice rats occur in great numbers, their runway threading the black mud covered daily by the tides, or rising into the higher ground which skirts the tidal zone. The abundance of these rodents, the ease of capture and their docile behavior in captivity, make them ideal laboratory animals. It is therefore surprising that so little has been recorded of their habits.

Observations on rice rats were made by Audubon and Bachman (1854), to which little has been added to the present day. Goldman (918) has presented a brief review of the habits of these rodents. Harper (1927) gives some interesting data on the nests and behavior of this species in the Okefinokee Swamp of Georgia, while Svihla (1931) has recorded observations on the Texas rice rat *(Oryzomys palustris texensis)*. Other than these accounts, published data on the life history of this widespread genus is all but lacking.

Rice rats range from New Jersey and the central part of the Mississippi Valley southward, being well represented in nearly every part of South America and reaching their greatest development in the tropics. More than 150 species and subspecies have been described, but little other than a name has been assigned to the majority of these, the habits having been totally unexplored.

While on a collecting trip in the south Atlantic States in September 1940, I visited Chincoteague Island, off the coast of Cape Charles, Virginia. Here I found rice rats very abundant and collected a good series. The following year I again visited this island, collecting from June 30 to July 3, 1941. Another series was taken, a number of live animals trapped for laboratory study and observations made on the habitat and general natural history of the species.

Habits

Superficially the rice rat bears a striking resemblance to the Norway rat. This resemblance is all the more realistic inasmuch as the two are often in the same habitat. Feral individuals of *Rattus* often occupy the same habitat in the marsh, particularly during the summer months, and the uninitiated is likely to mistake immature *Oryzomys* for *Rattus*. The rice rat may at once be recognized by the slimmer build, smaller, less prominent ears and eyes, relatively longer and more slender tail and the softer pelage. In addition, it lacks the "roman rose" of *Rattus norvegicus*. The infallible character may be found in the teeth, the tubercles of the upper molar crowns being in two series in *Oryzomys*, whereas, in *Rattus* they occupy three series.

Although rice rats are active at all periods during the day and night, they appear to move more widely and frequently during darkness. Possibly the character of the cover determines their movements. Under the dense stands

Fig. 1.—Habitat of *Oryzomys p. palustris* at Chincoteague, Virginia, Sept., 1940.
Fig. 2.—Feeding platforms of *Oryzomys* in habitat shown in Fig. 1.

of marsh grasses I trapped several *Oryzomys* in the middle of the day, and examination of their stomachs indicated that they had been feeding recently.

Severe winter storms and the frigid spells of coastal Virginia hold no fear for these rodents. Several muskrat trappers told me that they caught rice rats throughout the winter in their muskrat "sets."

In the southern states, rice rats and cotton rats *(Sigmodon)* are frequently found in the same association. In coastal Virginia, in the same habitat they are outnumbered only by *Microtus*. The little short-tailed shrew, *Cryptotis,* is also an inhabitant of the same marsh.

Oryzomys is an adept swimmer, diving and swimming under water for some distance. It has no particular modification for an aquatic life; the digital fringes are not well developed.

In eastern United States rice rats occur from the coastal swamps to dry fields at an elevation of a thousand feet or more. They are found in greatest numbers in the lowlands of the south Atlantic coast, being particularly abundant in the expansive marshes which border the bays. These rats occur in incredible numbers in the more suited localities.

Trails are not particularly well defined, as the dense vegetation of salt marsh grass *(Spartina alterniflora)* provides sufficient food everywhere and *Oryzomys* thus has no need of preparing runways to a source of food. Their presence may be noted by basal cuttings and the finely chewed or shredded outer layers of *Spartina* stalks.

In the areas which I studied, rice rats were feeding primarily upon the tender stalks of *Spartina,* and the branched stems of the glasswort, *(Salicornia europea).* The marsh habitat of these rats is partially flooded by the daily tides. Rice rats construct feeding platforms of the stems of marsh grasses, repairing to these to feed when tide water covers the mud flats. Large platforms approximate a dinner plate in size (Fig. 2). Audobon and Bachman refer to this species feeding on the Gama grass *(Tripsacum dactyloides)* and wild rye *(Elymus virginicus)* and note the penchant of captive individuals for meat. Indeed, like many other rodents, rice rats appear at times to be inordinately fond of flesh. Shantz (1943) has alluded to the flesh-eating proclivity of the rice rat, stating that at Smyrna, Delaware, these rats were feeding on the flesh of trapped muskrats. Captives which I possessed over a period of several months would eat the skinned bodies of *Peromyscus* and sparrows. In addition to flesh, *Oryzomys* apparently feeds upon snails and crustacea. The remains of fiddler crabs near their nests and small piles of the snail *(Melampus lineatus)* below the feeding rafts of *Oryzomys* suggest that these rats do feed on such animal matter as they can secure.

Most nests are constructed somewhat above tide level, although Audubon and Bachman report nests a quarter mile from dry ground, suspended in a bunch of interlaced marsh grass. These were breeding chambers for the reception of young. Those which I found were at the base of the marsh elder *(Iva frutescens)* or the groundsel tree *(Baccharis halimifolia).* Burrows which I suspected were occupied by *Oryzomys* (specimens were taken near the entrance) were shallow, seldom exceeding five inches in depth, and running somewhat less than a yard in extent, at variance with the observations of

Audubon and Bachman who state that burrows in the rice fields of the Carolinas and Georgia are seldom much below a foot in depth, at the end of which is a compact nest. All the nests I observed were slightly larger than a good-sized grapefruit, made of the material at hand, namely withered grasses, closely woven to form a compact dry chamber.

Rice rats are clean little rodents, spending much time on their meticulous toilet. They wet the back of their hands, then draw them over the ears and down over the face. The bottom of the feet are carefully licked, the tail is run lengthwise through the hands, while the rat nibbles gently on it. One hind foot is held by the fore paws while each toe is slowly licked and cleaned. The moistened claws are then used to preen the fur of the back, groin and shoulder. I have never seen any other small mammal so solicitous of its toilet.

Fig. 3.—Young *Oryzomys* approximately ten hours old.

Reproduction

Accounts of the breeding behavior of *Oryzomys* are notable only for the paucity of information. Bachman, who contributed the great wealth of data on small mammals in which he and the illustrious Audubon collaborated, states that the four or five young are born in April. Goldman remarks that three to seven young are produced at birth, four or five being the usual number. He further states that their appearance "at all seasons is ample evidence that there is no breeding season, except possibly near the northern limit of the group." Brimley (1923) records gravid *Oryzomys* in March, April, June, July August, September and November at Raleigh, North Carolina. He states that there are three to seven in a litter, averaging five. The nest, according to Brimley, is often built in cat-tails *(Typha)* surrounded by water. Svihla (1931) has described reproduction in *Oryzomys palustris texensis*. This subspecies apparenly produces somewhat smaller litters than typical *palustris*, for the Louisiana captives observed by Svihla averaged slightly more than three young to a lit-

ter. Of three adult females taken at Chincoteague, Virginia on September 5, 1940, one had seven 15 mm. embryos and was not nursing; another contained five 6 mm. embryos and was actively nursing, while a third, a large individual, was not pregnant nor had she recently nursed. Seven males taken at the same time had enlarged and descended testes. Thus some individuals under feral

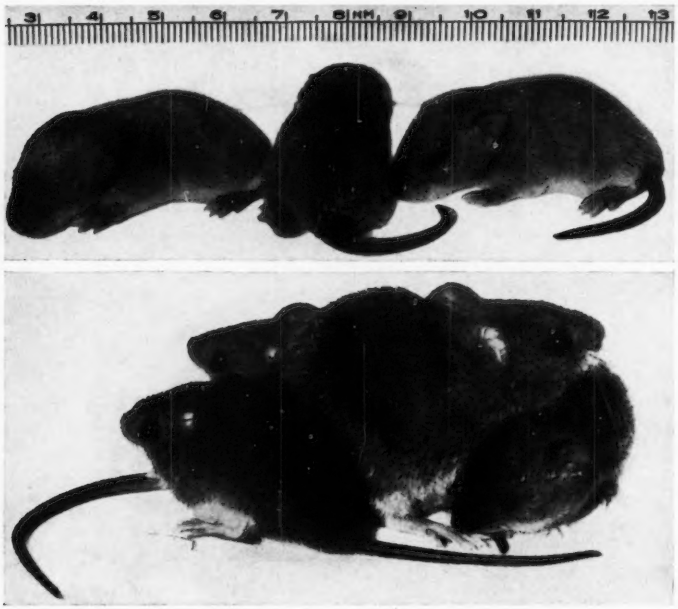

Fig. 4 (Upper).—Rice rats at six days. They are proportionately better developed than *Microtus pennsylvanicus* at this stage.

Fig. 5 (Lower).—These weaned young, with parent, are thirteen days old.

conditions breed immediately following parturition. This condition exists with captive animals. Svihla observed the gestation period of *texensis* to be twenty-five days, thus allowing fourteen litters a year if oestrous follows parturition, and a successful mating occurs. There is evidence that this fertility may occasionally be maintained in the wild state from March to early November in the northern part of the range; thus vigorous females could produce nine litters a season. The young, as will be shown, reach sexual maturity at an early age, the females capable of breeding when seven weeks old.

The following notes are based on a series of six litters born in captivity.

Birth.—At birth the young are flesh colored below, slaty above. Short gray hairs cover the upperparts and are best developed as 35 mm. vibrissae on the mystacial region and longer hairs on the flanks (Fig. 3). These can be seen

well only with a 7x magnification. The pinna is prominent, unfolded, but closed. The eye slit is very evident but tightly closed. Toes are well developed, with prominent claws, while the plantar tubercles are evident. The young rats have a very pronounced fold of skin from the base of the tail to the middle of the tibia .They are very active but the movements are not coordinated. Four new born rice rats averaged 3.7 grams. Measurements of the same group

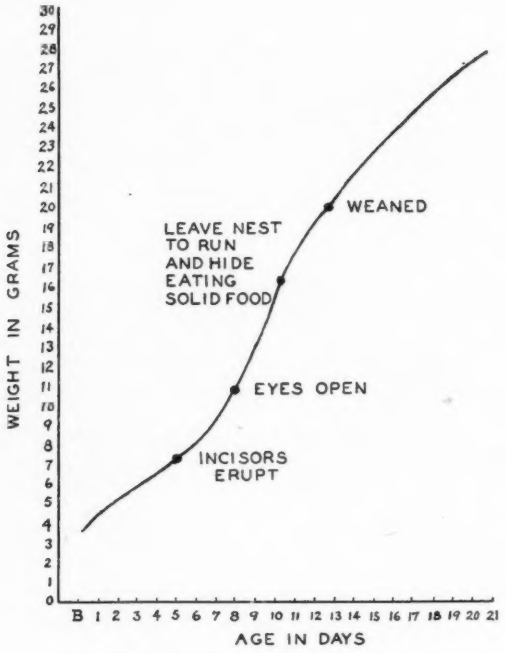

Fig. 6.—Development of rice rats.

average: total length, 61 mm.; tail, 19 mm.; hind foot 9 mm. A pronounced squeaking note can be heard at a distance of ten feet. Rice rats are developed in a slightly more advanced condition than *Microtus pennsylvanicus* at birth (Hamilton, 1941).

Two Days.—The dorsum of the young rats is noticeably darker than at birth, due to the pigmented hairs. The youngsters are very active and can actually crawl upright with some celerity, much more so than *Microtus* of comparable age. They emit a high pitched squealing, which greatly excites the mother. They now average 5 grams each.

Four Days.—The young rats are well covered dorsally with short hairs. The forehead is grayish brown, the shoulders dark gray washed with fulvous,

and the back dark gray. Numerous paler guard hairs grow from the rump and flanks. The underparts are naked. The squeaking of the young is very evident, sounding not unlike a bat. The young rats are able to crawl upright and average 6.3 grams. The measurements of seven from two litters average as follows; total length, 82 mm., tail, 30 mm., hind foot, 13 mm.

Six Days.—The youngsters are now well furred, grizzled, brownish gray above, with pale grayish white belly fur just appearing. The eight mammae on the females are quite apparent. Incisors in both upper and lower jaw cut the gums on the fifth day. Average measurements of 6 (2 litters) are: total length, 95 mm., tail, 36 mm., hind foot, 13 mm. Weight averages 7.5 grams (Fig. 4).

Eight Days.—Eyes open and very active, running about and leaving nest if disturbed. The young rats are now well covered with the sleek shiny juvenile fur, the belly grayish white, the back gray, the dorsal hairs tipped with chestnut. Feet white, the tail all black. Inside of ears light brown, the borders quite black but well furred. Average measurements of 5 (2 litters) are: total length, 103 mm., tail, 41 mm., hind foot, 15 mm. Average weight is 8.9 grams.

Ten Days. The youngsters leave their nest chamber to run about and eat solid food. They have a high-pitched reedy squeak. The mother is quite solicitous of her young, grasping them by the loose skin on the top of the head or back of neck. The young average 10.2 grams and the average measurements of five are: total length, 116 mm., tail, 47 mm., hind foot, 16.5 mm.

From the tenth day on, the young grow rapidly, being weaned on the eleventh to thirteenth day (Fig. 5). They gain about 1-1.5 grams a day until they are three weeks old, when the increase is somewhat slower.

Rice rats are half grown at two months (40 grams) and have attained their maximum growth at four months (50-80 grams). The development of young during the first three weeks of life is graphically illustrated in Fig. 6.

Oryzomys responds well to captivity, the animals breeding readily in confinement. It is desirable to keep this species in a humid atmosphere with plenty of water and sufficient green foods and vegetables.

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